THE GALAXIID FISHES OF NEW ZEALAND[1]

R. M. McDOWALL[2]

CONTENTS

ABSTRACT

Fourteen species in the family Galaxiidae are recognized from New Zealand, three fewer than in previous works. These are placed in two genera —Galaxias and Neochanna—as follows: Galaxias argenteus (Gmelin), G. fasciatus Gray, G. postvectis Clarke, G. brevipinnis Günther, G. vulgaris Stokell, G. maculatus (Jenyns), G. usitatus McDowall, G. gracilis McDowall, G. divergens Stokell, G. paucispondylus Stokell, G. prognathus Stokell, Neochanna burrowsius (Phillipps), N. apoda Günther, and N. diversus Stokell. This arrangement of taxa differs from previous arrangements in that lacustrine populations formerly known as G. lynx Hutton and G. koaro Phillipps are treated as synonyms of G. brevipinnis, G. anomalus Stokell is found to be a synonym of G. vulgaris and, although formerly placed in Galaxias, Neochanna burrowsius is regarded as showing much greater similarity to and affinity with the other neochannoid species and is accordingly placed in Neochanna.

Study of samples of the migratory juveniles of the diadromous species (G. argenteus, G. fasciatus, G. postvectis, G. brevipinnis, and G. maculatus) showed that although clear diagnostic characters for the juveniles of these species do not emerge, it is possible to distinguish species in mixed samples by means of modal differences in length at migration, head length, and body depth.

The diadromous species were found to have numerous small to moderate-sized eggs, to spawn mostly in the autumn and early winter, to spend larval and early juvenile life in the sea, and to

migrate into fresh water during the subsequent spring. *G. usitatus* and *G. gracilis* have forsaken the marine migratory habits (because of landlocking), but have numerous small eggs. The remaining seven species have few, larger eggs, spawn mostly in the winter and spring, and complete their entire life histories in fresh water.

The correlation between egg size, egg number, and life history pattern suggests selective advantage in having many small eggs, in species living initially in productive, marine plankton, and fewer, larger eggs in species living in flowing fresh water and not subject to the same type of dispersal away from the natal habitat.

There is a very obvious relationship between range and life history pattern—those species with marine life history phases are widespread in the New Zealand region and may occur on offshore islands and also in other, more distant land areas (Australia, South America). These species tend to have easily determined phylogenetic relationships with species outside the New Zealand region. Species restricted to fresh water have a much more restricted range and have largely cohesive distribution patterns, which can be mostly explained simply by known changes in New Zealand's geomorphology.

The age of the New Zealand galaxiid fauna is unknown. The family seems to have evolved in the Australasian region, since about 90 per cent of the species occur there. Phylogenetic relationships with the Retropinnidae and Aplochitonidae and a common origin for the three families in some early Northern Hemisphere salmoniform stock are suspected.

Phylogenetic relationships between Australian and New Zealand species can in many cases be established, and this, together with known marine life history phases, indicates that the New Zealand fauna is derived by transoceanic dispersal. The East Australian ocean current seems to provide a suitable mechanism for dispersal from Australia to New Zealand.

Although the New Zealand freshwater fish fauna is very small, there is no evidence that the present fauna represents only a fragment of a formerly larger fauna, reduced by marine transgressions that occurred during the early and mid-Tertiary, or by the glaciations of the Pleistocene. Though the fauna is small, and though the Galaxiidae represent a large proportion of the fauna, the family shows little evidence of radiation to fill the New Zealand freshwater habitats. Galaxiids are mostly solitary, stream dwelling, benthic, invertebrate feeding predators. They seem to show considerable sensitivity to alterations in the nature of the stream catchment and its vegetation cover.

The galaxiid fauna is easily and naturally divisible into a series of small species groups. *G.* *argenteus*, *G. fasciatus*, and *G. postvectis* are clearly closely related to each other, and to *G. truttaceus* in Australia. *G. brevipinnis* is very similar to, perhaps conspecific with *G. weedoni* in Tasmania, and is also probably ancestral to *G. vulgaris*. *G. maculatus* is common to Australia, New Zealand, and South America, and gave rise in New Zealand to *G. usitatus* and *G. gracilis*. *G. divergens*, *G. paucispondylus*, and *G. prognathus* form a very compact species group of an origin at present undetermined. *N. burrowsius*, *N. apoda*, and *N. diversus* are similarly very closely related and are perhaps derived from the Tasmanian neochannoid species, *G. cleaveri* and *G. anguilliformis*.

INTRODUCTION

The fishes of the family Galaxiidae are mostly small and scaleless, more or less benthic in habit, with rounded trunks and somewhat depressed, broad heads. Nearly all the species are secretive and solitary and have thick, fleshy fins. Some species are nocturnal, with free-ranging, pool-dwelling habits, and may exhibit some deepening of the trunk. A few species have mid-water shoaling habits, and these tend to have membranous fins and a more slender form.

The family Galaxiidae is very widespread in the Southern Temperate Zone, species occurring in Australia, New Zealand, South America, and South Africa, as well as on many islands in the vicinity of these land areas. Species abundance is greatest in Australia and decreases eastwards to New Zealand, South America, and South Africa in the pattern described by Fell (1962: 761). One species, *G. maculatus* (Jenyns), is found in Australia, Tasmania, Lord Howe Island, New Zealand, Chatham Islands, Chile, Patagonia, and the Falkland Islands, and is one of the most widely dispersed species of freshwater fish.

The family Galaxiidae is currently considered to belong to the order Salmoniformes (Greenwood et al., 1965: 394), comprising, with the families Aplochitonidae, Retropinnidae, and Salangidae, the suborder Galaxioidei. These four families are considered to constitute a distinctive radiation within the Salmoniformes. Var-

ious of the three southern families—Galaxiidae, Retropinnidae, Aplochitonidae—have at some time been related to the salmonoid or the haplomous fishes (Regan, 1909; Berg, 1940; Chapman, 1944; Gosline, 1960); the present consensus agrees that they have very definite salmonoid affinities (Weitzman, 1967; McDowall, 1969).

From the beginnings of galaxiid taxonomy late in the 18th century, the family has been a difficult and confused one. The morphology of the New Zealand species is plastic, and in many localities and some species groups, active speciation is occurring. The failure of earlier workers to take into account the rather distinctive juveniles, and the allometric growth that may succeed the juvenile stages, has led to repeated descriptions of some species. Lack of knowledge of the life history patterns and their relation to dispersal has resulted in description of fishes from apparently isolated localities as new. Repetitive description of well-defined species due to ignorance of earlier descriptions or mistaken identity has added to the problems, and confusion in the application of existing names has been considerable; e.g., Powell (1869), discussing the young stages of some *Galaxias* species, called them "smelt"—properly *Retropinna* in New Zealand—and published a figure that is clearly *G. maculatus* (Jenyns), labeling it *G. fasciatus* Gray.

Apart from a small paper by Hutton (1896) and Regan's (1905) revision of the whole family, the works of Stokell (1945, 1949) were the first serious attempt to define the New Zealand galaxiid species, and for the first time it became possible to identify adults of most of the species occurring in New Zealand. As a result of these and later papers by Stokell (1954, 1959b, 1960) and one by the writer (McDowall, 1967a), there are currently 17 galaxiid species recognized from New Zealand.

Studies of a New Zealand fishery based on species of *Galaxias* (McDowall, 1964b, 1965a, 1968b) showed that more meristic data and clearer diagnostic characters should be sought for adequate identification of some of the species, especially in their juvenile stages. Subsequent collections of many large samples of all the New Zealand species from a wide range of localities also suggested that there were some irregularities in their taxonomy. As a result of the present review, the number of species recognized is reduced to 14.

An attempt to determine species groups, phylogenetic patterns, and the evolution of the New Zealand galaxiid fauna is long overdue. It is also time that an attempt be made to relate the New Zealand fauna to the galaxiid faunas in Australia and South America. It is the objective of this study to attempt a synthetic analysis of the New Zealand Galaxiidae, to examine the manner in which galaxiid fishes appear to have invaded New Zealand's fresh waters and speciated there, and to determine the phylogenetic relationships of the species. Unfortunately, the systematics of the Australian and South American galaxiid faunas are not well known; studies of the species in these two areas will be necessary before the desired synthesis of the whole family can be accomplished.

MATERIALS AND METHODS

Material examined. A large collection of New Zealand Galaxiidae was studied, much of which was collected during a study of the biology of *G. maculatus* (McDowall, 1968b) or on specific field trips to collect certain species. Further material was collected by technicians at the Fisheries Research Division of the New Zealand Marine Department, and this was supplemented by samples in the collection of the New Zealand Dominion Museum. *Neochanna burrowsius* is a rare species that is difficult to collect, and my samples of this species were small; examples in the fish collections of the University of British Columbia and the National Museum of Canada were also
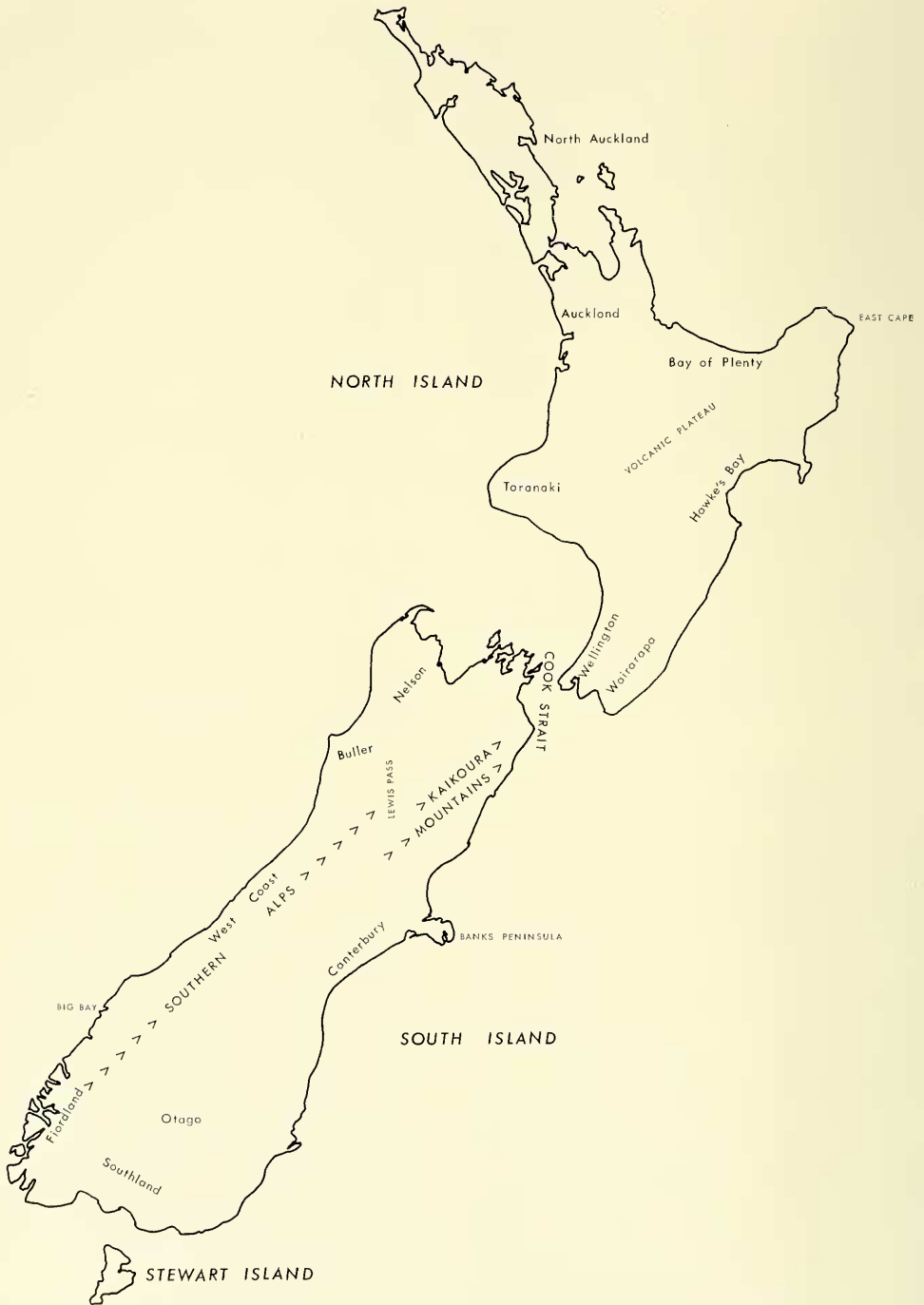
Figure 1. New Zealand place names—regions and physiographic features mentioned in text.

studied. For most species, large series were examined from a broad range of geographical localities. I have not listed in detail the material examined in the study, but in the distributional data for each species an asterisk is inserted by localities from which specimens were examined for meristic or morphometric data. The identifications of species from each locality are my own, except for a number reported by Fisheries Research Division biologists and technicians.

Museum abbreviations. In the listing of type specimens, the institutions at which the types are held are indicated by the following abbreviations:

AMS   Australian Museum, Sydney, Australia.

BMNH   British Museum (Natural History), London, England.

CMCNZ   Canterbury Museum, Christchurch, New Zealand.

DMNZ   Dominion Museum, Wellington, New Zealand.

GMUO   Geology Museum, University of Otago, Dunedin, New Zealand.

MCZ   Museum of Comparative Zoology, Cambridge, Mass., U. S. A.

MNHNP   Museum National d'Histoire Naturelle, Paris, France.

NZMD   New Zealand Marine Department, Fisheries Research Division, Wellington, New Zealand.

USNM   United States National Museum, Washington, D. C., U. S. A.

Sampling techniques. Galaxiid fishes are usually secretive, occupy deep cover, and are fast swimming; many species occur in very rapid, turbulent water. Thus they are usually difficult to capture. The principal tool used for collection was a small, back-portable electric fishing machine, which was used in all waters except estuaries where high salinities sometimes rendered it inoperable because of high water conductivity. Also, in some very pure mountain streams conductivity was very low and the effectiveness of the machine greatly reduced. The normal running time for one set of batteries—a pair of six-volt motorcycle batteries—was one and a half to two hours, although this depends on water conductivity. With two sets of batteries it was possible to spend a full day in the field without recharging. The effectiveness of the machine was greatest in shallow water, up to about 24 inches, and for the capture of solitary, cover-dwelling species. However, using the machine in conjunction with small seine nets, shoaling species were easily captured in large numbers. Paralyzed fish were usually retrieved with small metal gauze dip nets, but in torrential streams it was necessary to place a barrier, like a large dip net, a bag net, or a small seine across the stream flow, and chase the fish downstream towards the barrier with the electrode. For capturing shoaling fishes, a small, five-foot, one-man seine was constructed from fine-mesh mosquito netting strung between two bamboo poles; a length of light chain was used to weigh down the lower edge of the net.

Captured fish were immediately placed in a pail of water containing a narcotic—usually chlor-butol, occasionally "MS 222." Narcotizing the fish as they were caught prevented distortion due to asphyxiation and allowed long collection runs in the field without delays for fixing specimens. Whenever possible, the fish were fixed in the field, in shallow plastic photographic trays. The fish were spread out in the trays with minimal overlap and sufficient 10 per cent formalin poured on to cover but not float them. They were bottled when they had begun to harden. By this simple expediency, the difficulty of working with bent, twisted, and otherwise distorted specimens was almost completely avoided, and in general, the specimens were in excellent condition. After fixation for four or five days in formalin, the fish were washed for a similar period in several changes of tap water and transferred to 40 per cent isopropyl alcohol for storage.

Measurements and counts. Methods of measurement used were largely those de-

scribed by Hubbs and Lagler (1947: 13–15, figs. 3–5), in a few cases adapted to the particular morphological characteristics of the fishes studied. In most cases, measurements were taken with needle point dividers, although in large species vernier calipers were found to be more effective. In general, dimensions were determined to the nearest half millimeter. In small fish, and in measuring small dimensions, usually those less than 15 mm, and whose reference points are well defined, measurements were estimated to the nearest quarter millimeter. Frequently, accuracy of this degree is not warranted since the reference points are not clearly defined, and variations in body flexure at fixation and types of preservative used modify the body dimensions to an extent that makes accuracy of a quarter of a millimeter, and sometimes half a millimeter, quite meaningless.

Measurements were taken as follows: total length—either length to caudal fork (L.C.F.), or if the caudal is rounded, to posterior extremity of fin (T.L.); standard length (S.L.); body depth at vent (B.D.V.)—used instead of greatest body depth because the latter is greatly affected by sexual maturity and distension of the stomach after feeding; depth of caudal peduncle (D.C.P.); length of caudal peduncle (L.C.P.); predorsal length (Pre-D.); preanal length (Pre-A.); length of bases of dorsal and anal fins (D.F.B. and A.F.B.); maximum length of dorsal and anal fins (D.F.M. and A.F.M.); pectoral fin length (Pec.); pelvic fin length (Pel.); pre-pelvic length (Pre-Pel.); pectoral-pelvic length (Pec.-Pel.); head length (H.L.)—measured to edge of opercular membrane; head depth (H.D.)—an uncertain measurement, but taken vertically at the ridge across the nape which represents the posterior margin of the cranium, the position of which can be determined by running the finger forwards across the top of the head; head width (H.W.); snout length (Sn.L.); postorbital head length (P.O.H.L.); interorbital width (Io.W.)—fleshy interorbital; diameter of eye (D.E.)—horizontal fleshy eye diameter, not bony orbit; length of upper jaw (L.U.J.); length of mandible (L.M.); width of gape (W.G.).

The following structures were counted: fin rays in the dorsal, caudal, anal, pelvic, and pectoral fins; vertebrae; gill rakers on the first arch; branchiostegals; pyloric caeca. Counting fin rays in galaxiid fishes presents a minor problem, since a variety of types of soft rays occurs. As in all the salmonoid fishes, procurrent rays are present in the dorsal, anal, and caudal fins. Hubbs and Lagler (1947: 9) recommended the inclusion of these rays in the counts of the dorsal and anal fins of salmonoids. In the Galaxiidae, such a procedure is a problem, since the anteriormost rays are usually deeply embedded in the opaque, fleshy fin bases and accurate counts are impossible without staining. Use of alizarin stain techniques showed that in the dorsal and anal fins there are from one to five of these rays, varying in size from a tiny, little-ossified splint, to a strongly-ossified but unbranched and unsegmented ray. Accordingly, the counts given in the subsequent descriptions are, in all cases, of segmented rays, whether branched or not. This procedure, which enables accurate and standardized counts, is more or less equivalent to the principal ray count, although sometimes a segmented, unbranched ray is counted, which does not quite reach to the distal margin of the fin, as it should to be counted as a principal ray. In the paired fins, the situation is a little simpler and more stable. Occasionally one unbranched but segmented ray is present in the medial border of the pectoral and pelvic fins, and this was counted, together with the larger branched rays. The small, unsegmented splintlike ray, more rarely present in these fins, was not counted.

Vertebral counts were taken as excluding the urostylar vertebra and hypural plate. Their inclusion would increase the count by one or two, depending on whether the

urostylar elements were fused or not; the condition was found to be variable. All branchiostegals, including those which do not have a definite attachment to the hyoid arch, were counted. Gill rakers were counted in the conventional manner, the raker at the angle between the epibranchial and ceratobranchial, which does not associate with either bone, being counted with the lower limb.

All counts were made using a dissecting stereomicroscope. In many cases, samples were sufficiently large to allow preparation of cleared, stained skeletal preparations. X-rays were also used extensively for vertebral counts.

Clearing and staining. During the early part of the study, the potassium hydroxide clearing technique of Hollister (1934) was employed. Later, the clearing method developed by Taylor (1967), in which trypsin is utilized for the digestion of body tissues, was used. The principal advantage of this method is that the problem of explosion and distortion of fish and the fragmentation of old specimens is largely avoided. In addition, clearing is accomplished more rapidly than in other techniques, and distorted, asphyxiated specimens are often partially relaxed.

SYSTEMATICS

FAMILY GALAXIIDAE

The family Galaxiidae was formed by Müller (1844) to contain the genus *Galaxias* Cuvier, 1817. Osteological study is becoming imperative for understanding the relationships of the species within the family, as well as among the Galaxiidae and the Retropinnidae and Aplochitonidae, and the relationships of the three families with the broader sphere of the isospondylous fishes. The present synopsis hopefully forms an initial basis for determining the limits of the family.

Diagnosis. Medium-sized to small fishes (3–60 cm) with 0–3 rudimentary to well-developed pyloric caeca. Both gonads developed, although the left may be larger than the right, ovaries gymnoarian. Urinogenital aperture on a papilla set in a post-anal depression. Sexes similar, male nuptial tubercles not present, but in many species sensory tubercles present on the head and pectoral fins in both sexes. All the species except one are believed to breed in fresh water, the exception in river estuaries. Some species are confined to fresh water, either lacustrine or fluviatile, others are amphidromous with marine juveniles.

Scales lacking, lateral line well developed, an accessory lateral line present dorsolaterally in some species.

Pelvic fins abdominal, 4-8 rays, usually 7, or fin absent. Caudal fin emarginate to rounded, rarely forked, usually 16 principal rays (14 branched), procurrent rays well developed along caudal peduncle and anterior to dorsal and anal fins, dorsal and anal fins originate well back on trunk. Vertebrae 37–64, branchiostegals 5–9.

Maxilla partly included in gape, toothless; teeth on premaxilla and dentary uniserial, mesopterygoidal, basihyal, and pharyngeal teeth developed (reduced or absent in *Neochanna*). No supramaxilla; no vomerine teeth.

Parietals large, uniting broadly in a median suture, supraoccipital not in contact with frontals and excluded from foramen magnum. Posterior myodome open. Orbitosphenoid, basisphenoid, and proethmoids absent; supraethmoid and ventral ethmoid present. Posttemporal simple; no mesocoracoid; postcleithrum present or absent. Epipleural and epineural ribs present (except in *Neochanna* and *Nesogalaxias*); neural and haemal arches autogenous, anterior uroneural not fused with terminal vertebra, none of terminal vertebrae upturned. Caudal neural and haemal spines much compressed.

General and diagnostic characters

Fishes of the family Galaxiidae present a varied but distinctive facies. The first observers (Forster, 1778; Bloch and Schneider, 1801) saw a resemblance to the
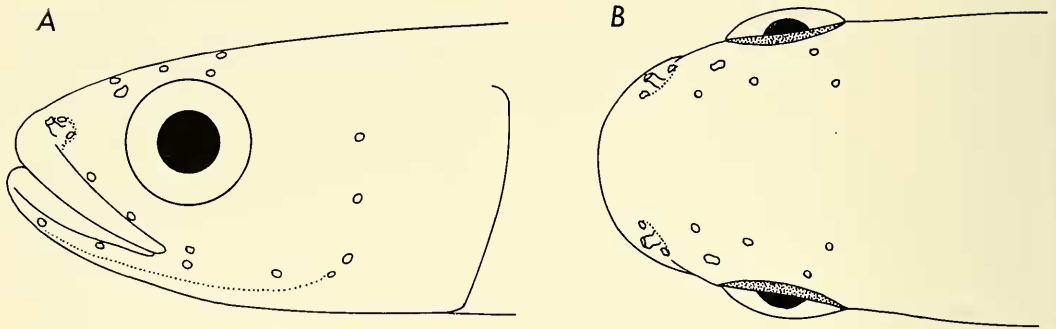
Figure 2.   Distribution of laterosensory pores in a generalized galaxiid. A, Lateral head; B, Dorsal head.

Northern Hemisphere pikes (family Esocidae), probably because of the extremely posterior position of the dorsal and anal fins and the long jawed appearance of the single species with which they were acquainted. However, these similarities are superficial. The fishes in the family are scaleless, with thick, highly mucigerous, leathery skins. The head is usually moderately large, with prominent jaws, the upper and lower varying in proportional development so that the lower may protrude, recede, or be equal in length to the upper. Lateral line pores on the head are well developed. In New Zealand representatives, the disposition of these pores is fairly constant, with only occasional individual variations in pore number (Fig. 2). Their disposition can be related to the supra-orbital, infra-orbital, and hyomandibular branches of the lateral line system of the head (see Lagler et al., 1962: 391).

The lateral line is well developed on the trunk from the upper edge of the opercular aperture to the middle of the tail base. It consists of a series of superficial papillae, set in a midlateral furrow, which may be well defined, especially caudally. In some species groups there is a dorsal accessory lateral line along the dorsolateral trunk, evident as a more or less distinct linear series of small, widely-separated papillae from the occiput to about the dorsal fin.

The nostrils are well developed, the anterior one set in a small depression and tubular. In *Neochanna* it is especially well developed, sometimes extending forward beyond the upper lip. The posterior nostril is a simple aperture.

The form of the mouth varies, the profile of the jaws from the ventral aspect varying from deep and narrow, U-shaped, to broad and shallow, with depth much less than breadth (Fig. 3). In the adults of most species, the head, anterior trunk, and pectoral fins and fin bases are covered with small papillae. These are unlike the papillae of the Percidae, which are somewhat horny in nature, or those in the Retropinnidae, which are much better developed and more widespread. They are unusual in that they are present equally in both sexes. Although a directly reproduction-related function cannot be ruled out, the bisexual occurrence of these papillae, apparently in all seasons of the year, suggests a sensory function, which may or may not be related to reproduction. These papillae do not appear to be connected with the lateral line system, as is the case in the head papillae in many fishes. Papillae of this type do not appear to have been discussed in the literature, and their function is at present obscure.

The dorsal and anal fins are positioned posteriorly, and when depressed against the trunk, may overlie the base of the caudal fin; the anal fin is more or less below the dorsal. These fins are variable in their size and shape, usually short-based,
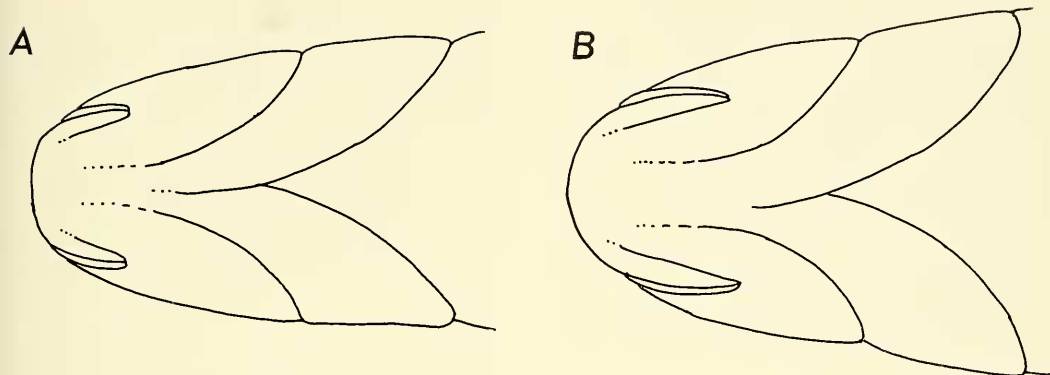
Figure 3.   Ventral profile of jaws.   A, Broad and shallow—as in *Galaxias divergens;* B, Narrow and U-shaped—as in G. *fasciatus.*

sometimes high and rounded, but in other cases much lower and not extending back much beyond the fin base. The caudal fin varies from well-forked to much-rounded. The pelvic fins are usually rounded in shape and expansive. The pectoral fins are variable in length and position and may be quite high laterally, with the blade of the fin vertical, or low lateroventrally, with the fin lamina more or less horizontal. In most species all the fins are thick and fleshy, especially at the bases.

Teeth are present on the premaxilla, mandible, basihyal, mesopterygoid, the pharyngobranchial of the third, the epibranchial of the fourth, and the ceratobranchial of the fifth branchial arches. The basibranchial plate is toothless. Teeth on all but the basihyal and the pharyngeal bones are uniserial; regularly in some species and in occasional individuals in others, however, there is a tendency for teeth to be displaced laterally from the primary row, appearing biserial. Mesopterygoidal teeth are reduced or absent in the neochannoid species. The teeth are usually conical, but in *Neochanna apoda* the mandibular and maxillary teeth are peculiarly flattened and incisorlike. This condition does not occur in any other galaxiids. In many species the jaw teeth are enlarged laterally as opposing groups of canines. Associated with the toothed bones are unattached, or decumbent teeth, which usually lie freely in the tissues covering the bones.

The structure of the ovaries in the Galaxiidae was described as gymnoarian by Hoar (1957: 289). Kendall (1922: 202) examined the "oviducts" of some salmonoids and concluded that they are shallow, open troughs and not entirely lacking, and that they are not radically different from those of other isospondylous fishes. However, the reduced condition of the oviducts, as in the Salmonidae, persists throughout the salmoniform fishes, and the condition is sufficiently distinct for Hoar to distinguish them from other ovarian types. Breder and Rosen (1966: 614) followed Hoar, stating that in the Galaxiidae and other salmonoids, the "ova pass into the peritoneal cavity and thence through the pores to the exterior." Henderson (1967: 447) concluded that the eggs of Salmonidae are discharged into the abdominal cavity, and that proper oviducts are lacking.

The New Zealand Galaxiidae exhibit considerable morphological plasticity. Most characters were found to vary from species to species, and even usually stable characters, like pelvic and caudal fin ray number, were found to differ in several phylogenetic lines. Stokell (1945:475) considered vertebral number to be the most important taxonomic character. This has

proved to be a useful character, but it is very important to bear in mind the temperature differences that occur along the 900 mile north-south axis of New Zealand— 34 1/2 to 47 degrees south latitude—and the effect of temperature on vertebral number.

Apart from vertebral number, important meristic characters included number of caudal, anal, pelvic, and to a lesser extent, pectoral and dorsal fin rays. The number of gill rakers and branchiostegals exhibits interspecific variation.

The most important morphometric characters were the following: length and depth of caudal peduncle, relative positions of the dorsal and anal fins and their basal and maximal lengths, lengths of pectoral and pelvic fins, head length, eye diameter, lengths of upper and lower jaws, width of gape. The development of canine and mesopterygoidal teeth, pyloric caeca, and gill rakers exhibits interspecific variation.

In some species groups, color pattern is diagnostically important: e.g., *G. fasciatus* Gray, *G. argenteus* (Gmelin) and *G. post-vectis* Clarke are similar in form but can be separated immediately and reliably by color pattern alone. In other species groups, specific differences are clearly indicated by fundamental differences in the life history pattern: e.g., *G. brevipinnis* Günther has marine or lacustrine whitebait juveniles, whereas *G. vulgaris* Stokell, which is morphologically quite similar, has no whitebait stage.

Most of the taxonomic characters used are completely conventional in ichthyology, but the morphological plasticity of the Galaxiidae results in a considerable diversity of such characters. Some of these are stable and unimportant throughout much of the family although they show significant variation in certain species or species groups (e.g., pelvic fin ray number, snout length), but other characters vary widely throughout the New Zealand members of the family.

Generic classification

Seven generic names have been applied to New Zealand galaxiids. Two of these involve now obvious errors—the use of *Esox* by early workers and the failure of Jenyns (1842: 118) to recognize the previously published genus *Galaxias* when he described galaxiid species in a new genus *Mesites*, a name further invalidated by preoccupation for a genus of beetles (Schoennherr, 1838). These two names are clearly not applicable to galaxiid fishes and present no nomenclatural or taxonomic difficulties.

The type genus for the family is *Galaxias* Cuvier, 1817, for which the type species is *G. fasciatus* Gray, 1842 (see McDowall, 1967b). Günther (1867: 306) described a galaxiid mud-fish in a new genus *Neochanna*, which was distinguished chiefly by the absence of pelvic fins. In 1899, Ogilby placed *G. attenuatus* (Jenyns) in a new genus *Austrocobitis*, distinguished from *Galaxias* by the form of the trunk, the small fins, and the forked caudal. Whitley (1935, 1956a, b) has consistently used *Austrocobitis*, but Stokell (1945: 124) claimed that these characters are widespread amongst divergent groups of galaxiids and that these species do not form a natural grouping. *G. attenuatus* [=*G. maculatus* (Jenyns)] and its New Zealand and Australian derivatives do have characters that set them apart from the rest of the family. However, at present I think that a broad generic revision of the family is necessary, and, thus, that it is inappropriate to make generic changes of this type here.

Scott (1936) proposed a reorganization of the family at subfamilial, generic, and subgeneric levels. In this paper he placed *G. burrowsius* Phillipps in a new genus *Saxilaga*, distinguished by the lack of mesopterygoidal teeth and the presence of pelvic fins (cf. *Neochanna*, which usually lacks both, and *Galaxias*, which has both). Stokell (1945: 129) correctly showed that *G. burrowsius* sometimes has mesopterygoidal teeth, though they are reduced in

size and number. In this paper (p. 134) he listed *Saxilaga* as not recognized and later (1949: 481) described Phillipps's species in the genus *Galaxias*. Phillipps (1940: 39) included this species in the genus *Paragalaxias* Scott, but this is clearly an error since Scott (1936: 87) defined *Paragalaxias* as having the dorsal fin well forward, over the pelvic fins. The allied problem of the validity of the genus *Paragalaxias* need not be considered here.

Scott (1966) reasserted the validity of his generic arrangement of the family. For *Saxilaga*, he noted (p. 250) that "further investigations have shown that certain diagnostic features originally described as absolute probably are not so." He maintained that *Saxilaga* is a good genus for *G. burrowsius* Phillipps, *G. globiceps* Eigenmann, and *G. anguilliformis* Scott, but noted that "if *Saxilaga* is to be maintained, modal and not absolute criteria are to be accepted for these features." He assembled a series of characters that he considered to unite the three species—"elongate body, small eye, small head, reduced number of pelvic fin rays (modally five or six), paired fins short, vertical fins low, squarish, their rays compressed with or without branching . . . . anal continuous or sub-continuous with caudal ridge which is well developed, high, caudal rounded or sub-truncate, fish heavily pigmented . . . . taken collectively, they appear to constitute a significant constellation."

Scott's practice of basing generic divisions on apparently plastic, adaptive, and often widespread characters leads to problems that suggest that such generic divisions are better abandoned. Examination of the distribution of galaxiid genera as he uses them produces the following patterns: *Saxilaga*—Tasmania, New Zealand, South America; *Brachygalaxias* Eigenmann, according to Scott's arrangement—South America, Australia. If we are to use the genus as a collective grouping for species comprising several similar independent radiations from the central stock of the

family, then Scott's genera are proper. However, I think that our understanding of the family is better served if we use the taxon to express phyletic relationships. If the species in these two genera are phyletically related, these patterns raise considerable zoogeographic problems, since all the species included belong to groups which, now at least, are found only in fresh water and none of which belong to the much more easily dispersed diadromous species groups. This association of morphological peculiarity with restriction to fresh water has important implications. First, since these species are restricted to fresh water, their ability to disperse is probably lower than that of diadromous species. Second, the fact that they are restricted to fresh water suggests that their common morphological peculiarities may be related to independent development of adaptations to specialized freshwater habitats, as is possibly the case in the mud fishes in Tasmania and New Zealand. I think that some of the similarities that Scott has used to draw species into generic groups are convergent adaptations to similar modes of life (however, see p. 425, where dispersal and phylogeny are discussed).

Scott (1966: 253), discussing the subfamilial classification of the family, suggested that "a more natural division of the family would appear to involve the association on one hand of forms with more than 50 vertebrae and on the other hand of forms with fewer than 50 vertebrae." *G. gracilis* McDowall from New Zealand has 47–50 vertebrae, the lowest number recorded for the family in New Zealand. This species is almost certainly derived from *G. maculatus* (Jenyns), which has 59–64 vertebrae, the maximum for the family in New Zealand. Thus, in this simple case of landlocked speciation, *G. gracilis* has traversed the full range of vertebral number for *Galaxias* in New Zealand. According to Scott's proposal, it has thus moved from one subfamily to the other. Bearing in mind the effect of temperature on verte-

bral number, it is clear that this is not a useful character at the subfamilial, or even generic level. Scott (1966) also made use of pelvic fin ray number, combining species that exhibit reduction in the number of rays from the usual seven. I do not think that this is a useful character either. Within the New Zealand Galaxiidae alone, reduction in pelvic fin ray number has almost certainly taken place in three widely divergent lines—those leading to *N. burrowsius* (Phillipps), *G. divergens* Stokell, and *G. usitatus* McDowall. I think there is a need for the generic classification of the family to be based on more fundamental characters than vertebral and pelvic fin ray number, and for the classification to better express natural groupings and phylogeny. For these reasons, only two genera are recognized for the New Zealand Galaxiidae in the present study—*Galaxias* Cuvier and *Neochanna* Günther, following Stokell (1945, 1949).

KEY TO GENERA

Mesopterygoidal teeth, epipleural ribs, supraethmoid and ventral ethmoid present, pelvic fins six or more rays . . . . *Galaxias*

Mesopterygoidal teeth reduced or absent, epipleural ribs, supraethmoid and ventral ethmoid absent, pelvic fins five or fewer rays, or fins and girdle absent. . . . . *Neochanna*

GALAXIAS CUVIER

Galaxias Cuvier, 1817: 183 (type species *Galaxias fasciatus* Gray by subsequent monotypy).

Mesites Jenyns, 1842: 118 (type species *Mesites attenuatus* Jenyns 1842 by subsequent designation, Jordan, 1919: 212, preoccupied by *Mesites* Schoenmherr, 1838, Coleoptera).

Austrocobitis Ogilby, 1899: 158 (type species *Mesites attenuatus* Jenyns, 1842 by subsequent designation, Whitley, 1956a: 34).

Diagnosis. Trunk cylindrical to a little compressed, naked; dorsal fin origin very posterior, about above vent. Pelvic fins present, six to eight rays, commonly seven; pectoral fin positioned laterally to low lateroventrally. Caudal fin usually with 16 principal rays, sometimes reduced to 15 or fewer. Jaw teeth conical, uniserial, with or without canines; mesopterygoidal teeth

well developed to rudimentary, uniserial; lingual teeth biserial. Median supraethmoid and ventral ethmoid present; postcleithrum present or absent; epipleural ribs present.

KEY TO SPECIES OF *GALAXIAS*

This key is adapted from McDowall (1966b), incorporating taxonomic changes made since that time and those proposed in the following pages.

1. Lower jaw much longer than upper .... *G. prognathus*, p. 393.
   Lower jaw not much longer than upper ... 2.
2. Lower jaw much shorter than upper, tucks behind upper when mouth closed 3.
   Jaws sub-equal, lower if shorter not tucking behind upper .... 4.
3. Canine teeth strongly developed .... *G. brevipinnis* p. 363.
   Canine teeth lacking .... *G. postvectis* p. 361.
4. Pyloric caeca long, length much greater than breadth .... 5.
   Pyloric caeca short to absent, usually short stubs .... 6.
5. Vertebrae 49–57, gill rakers 9–13, depth of caudal peduncle usually much less than length .... *G. vulgaris* p. 372.
   Vertebrae 58–61, gill rakers 14–17, depth of caudal peduncle sub-equal to length .... *G. argenteus* p. 352.
6. Canines well developed ... *G. fasciatus* p. 355.
   Canines lacking or weak .... 7.
7. Gill rakers very short, 11 or fewer .... 8.
   Gill rakers long, 11 or more .... 9.
8. Usually six pelvic rays, 15 caudal rays .... *G. divergens* p. 384.
   Usually seven pelvic rays, 16 caudal rays .... *G. paucispondylus* p. 390.
9. Gill rakers up to 17, vertebrae 54 or more .... 10.
   Gill rakers 18–23, vertebrae 47–50 .... *G. gracilis* p. 384.
10. S.L./H.L. 22.0–24.6%, 54–59 vertebrae .... *G. usitatus*, p. 382.
    S.L./H.L. 18.5–21.6%, 59–64 vertebrae .... *G. maculatus* p. 378.

Galaxias argenteus (Gmelin, 1789)
Figure 4

Esox argenteus Gmelin, 1789: 1393 (holotype: unknown; locality: a small lake in Dusky Bay (Dusky Sound?), New Zealand.)

Esox alepidotus Bloch and Schneider, 1801: 395 (replacement name for *E. argenteus* Gmelin, 1789): Cuvier, 1817: 184; Forster, 1844: 142.

Galaxias alepidotus: Richardson, 1843: 25; Dieffenbach, 1843: 219; Richardson, 1848: 77; Günther, 1866: 208; Hutton, 1872: 58; 1889:
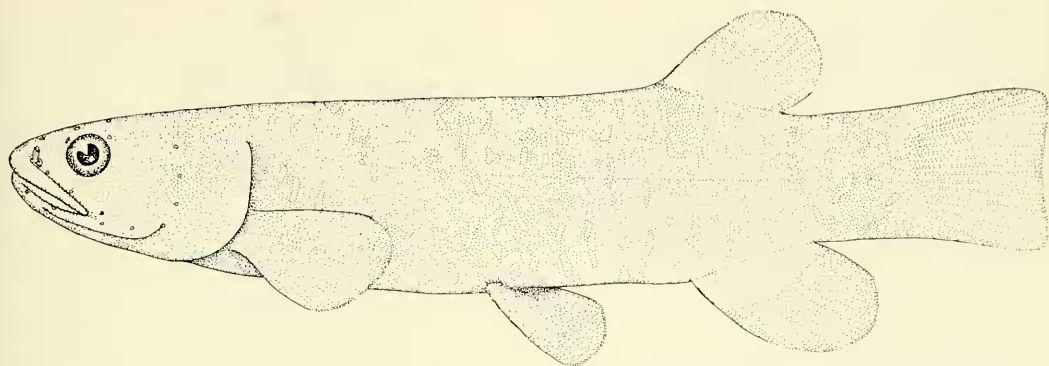
Figure 4. *Galaxias argenteus* (Gmelin), 280 mm L.C.F., Little Waitangi Stream, Pauatahanui Inlet.

284; 1896: 317; 1904: 51; Regan, 1905: 375; Waite, 1907: 12; Phillipps, 1927a: 13; Stokell, 1949: 493; 1954: 419.

Galaxias forsteri Valenciennes, *In* Cuvier and Valenciennes, 1846: 531 (replacement name for *Esox alepidotus* Bloch and Schneider, 1801).

Galaxias grandis Haast, 1872: 278 (holotype: apparently lost, see Stokell, 1949: 493; locality: creeks near Lake Ellesmere); Hutton, 1874: 107; 1904: 51.

Galaxias kokopu Clarke, 1899: 88 (holotype: unknown; locality: western slopes, South Island); Hutton, 1904: 51.

Galaxias argenteus: Whitley and Phillipps, 1940: 230 (partim); Stokell, 1960: 235.

Diagnosis. Differs from *G. fasciatus* Gray (Fig. 6) in coloration and in having very strongly developed pyloric caeca, longer head, more posterior pelvic insertion, higher depth of caudal peduncle/length of caudal peduncle ratio and jaw in head ratio (i.e., longer jaws), eye further forward in head and somewhat higher pectoral fin ray counts. Overlap in most of these characters is considerable and coloration is the most useful character. *G. argenteus* has numerous, small, irregular, gold spots on the dark trunk, while *G. fasciatus* has more regular vertical pale bands.

Differs from *G. postvectis* Clarke (Fig. 9) in coloration, in having stronger development of canine teeth in the jaws, much longer head and jaws, the jaws subequal, the eye further forward in the head, longer anal fin base, more posterior pelvic fin insertion, more anal fin rays, and somewhat higher numbers of branchiostegals and gill rakers. Coloration is again the most useful means of differentiating these species, jaw length, especially the shortened lower jaw in *G. postvectis* also enabling easy separation.

Description. Stout bodied, trunk somewhat rectangular in section and flattened dorsally, mid-dorsal groove moderately to well developed. Trunk deep, deeper than broad, greatest depth at or in front of pelvic fins. Depressed dorsally on head, considerably compressed posteriorly on caudal peduncle which is very short and deep, usually deeper than long. Lateral line an indistinct lateral furrow; accessory lateral line present but difficult to distinguish. Head very long, a little broader than deep. Eye moderately large and set moderately deep on lateral head, eye diameter/head length ratio not high because of great length of head; interorbital convex, very broad; jaws about equal, prominent. Lips thick and fleshy; cleft of mouth moderately oblique, reaching to between middle and posterior margin of eye. Profile of lower jaw from ventral aspect deep and rather narrow, U-shaped. Canine teeth well developed laterally in both jaws; mesopterygoidal teeth strongly developed; gill rakers long; pyloric caeca strongly developed.

Unpaired fins well developed, with thick fleshy bases; dorsal base of moderate

length, anal base long; both fins have greatest fin length much exceeding basal length, with rounded distal margins. Dorsal fin set well back, anal origin below or a little behind dorsal origin. Pectoral fins moderately long but not expansive, fleshy, inserted moderately low lateroventrally. Pelvic fins very long, expansive, and fleshy. Caudal fin long, thick and fleshy, depth noticeably less than body depth; truncated or a little emarginate in small specimens; caudal peduncle flanges well developed, extending forward almost to anal fin insertion.

Variation. Meristic: dorsal 10 (16), 11 (21), 12 (2); caudal 15 (1), 16 (38); anal 12 (13); 13 (20), 14 (5), 15 (1); pelvic 7 (38), 8 (1); pectoral 13 (7), 14 (27), 15 (5); branchiostegals 7 (2), 8 (33), 9 (4); vertebrae 58 (4), 59 (16), 60 (15), 61 (2); gill rakers 4–10 (3), 4–11 (7), 4–12 (1), 5–10 (4), 5–11 (21), 5–12 (2). Morphometric: see Table 1, p. 358.

Coloration. Often dark, a deep gray-brown, sometimes paler, approaching a buff color. The head, dorsal and lateral trunk, and fin bases are profusely covered with delicate, gold spots, lines, crescents and rings. These tend to be finer dorsally and on the head, coarser and bolder on the trunk. The belly is usually paler, bluish gray in dark examples, correspondingly lighter in paler specimens. A bluish blotch is present above and behind the pectoral fin base, but in heavily pigmented fishes it is of similar color to the trunk and is indistinct.

Size. Clarke (1899: 83) reported that *G. kokopu* (= *G. argenteus*) grows to 23 inches (584 mm) and a weight of six pounds. Haast (1872: 278) recorded a specimen 19.3 inches (490 mm) and Stokell (1949: 494) one of 17 inches (432 mm). *G. argenteus* is thus reliably reported to grow to much greater size than any other galaxiid, although large examples are now very rare. The largest specimen I have seen was 330 mm and others were commonly up to about 280 mm long.
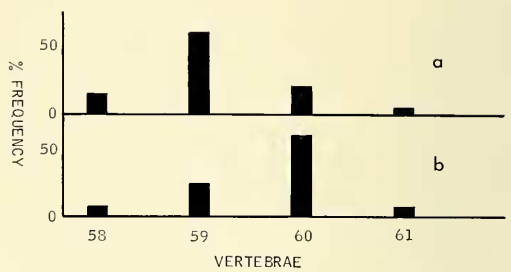

Figure 5. Variation in vertebral number in *Galaxias argenteus*. A, Localities in the southwest of the North Island —Wellington District (20 examples); B, Localities in the west of the South Island (17 examples).

Population differences. There was little scope amongst the few specimens examined for revealing regional variation in *G. argenteus*. From grouping samples from the Wellington Province, and those from the west coast of the South Island, there appears to be slight displacement in dorsal fin ray number, the northern examples having modally fewer rays than those from the south. A similar displacement in vertebral number is evident (Fig. 5). These differences are slight, but further study of more adequate samples may confirm the southward increase in meristics hinted at here.

Habitat. *G. argenteus* is exclusively lowland in range, inhabiting pools in lowland swamps and streams. It is an uncommonly seen species, usually lurking beneath cover, and is probably nocturnal, feeding in more open water during the night. Haast (1872: 278) reported catching *G. argenteus* of large size from very small streams, and such waters appear to be a characteristic habitat, especially when overgrown with flax (*Phormium tenax*) and raupo (*Typha angustifolia*). Collections from the west coast of the South Island have shown that *G. argenteus* is sometimes common in flax swamps and also occurs in the bush-stained, tea-colored streams there. It has also been taken from Lake Brunner (G. A. Eldon, pers. comm.) and may be more common in shallow weedy lakes than present records indicate.

Life history. Specimens of *G. argenteus* collected in March included a female approaching maturity and a ripe male. Others collected during September to December had very immature gonads. These data suggest autumn or early winter spawning. *G. argenteus* has a whitebait juvenile comparable with juveniles of *G. fasciatus* and *G. postvectis*, which migrates into fresh water during the spring. These species with whitebait juveniles migrate upstream together, and this suggests that they may spawn at about the same time, during the autumn or early winter.

Nothing is known of the spawning locality, although spawning migrations are not suspected. The eggs of the female approaching maturity were too small for useful size determination, but this fish, 251 mm long, contained about 11,000 eggs.

After hatching, the larvae are probably carried downstream to the sea, where larval and juvenile development occurs. At their subsequent upstream migration, the whitebait of *G. argenteus* are transparent, with very little pigmentation (Fig. 43) and are comparatively large (50–55 mm). Soon after migration, trunk pigmentation increases and intensifies to a dark gray-brown, eight to ten pale blotches or bands develop across the lateral trunk, and the adult pattern finally becomes superimposed on the juvenile banding. The stout, deep-bodied form of the adult is rapidly attained.

Distribution. *G. argenteus* is widely distributed in lowland localities that are accessible from the sea. It is known from the following: Mokau River (Fig. 7: 25); Pokaka Stream (27); Waikawa Stream (32*); Waikanae River (36*); Whareroa Stream (39*); Horokiri Stream (40); Little Waitangi Stream (41*); Trotter's Gully Stream (44) and Hawkin's Gully Stream Stream (45*), Makara System; Belmont Stream (48) and Moonshine Stream (42), Hutt System; York Bay Stream (51*);

Day's Bay Stream (53); Wainuiomata River (50); Wairarapa (55, Stokell, 1949: 494); tributaries of Lake Ellesmere (89, Haast, 1872: 278); Mokihinui River (69); Buller River (71); Grey River (72); Lake Haupiri (73); Lake Brunner (74*); Lake Kaniere (77); Lake Ianthe (79*); Whataroa River (80*); Lake Paringa (81, Haast, 1872: 278); Moeraki River (82); Dusky Bay (86, Dusky Sound?, type locality, Forster, 1778: 159); Stillwater River (87); Milford Sound (85, Hutton, 1896: 317); Southland (91, Stokell, 1949: 494); Horseshoe Bay Creek (93); Chatham Islands (94, Skrzynski, 1967: 95).

Galaxias fasciatus Gray, 1842
Figure 6

Galaxias fasciatus Gray, 1842: 73 (syntypes (3): BMNH 1967.8.14.9–11, not seen; locality: River Thames, New Zealand); Dieffenbach, 1843: 221; Valenciennes, *In* Cuvier and Valenciennes, 1846: 350; Richardson, 1843: 25, 1848: 77; Günther, 1866: 209; Kner, 1865: 319; Hutton, 1872: 59; Clarke, 1899: 90; Hutton, 1904: 51; Regan, 1905: 374 (partim); Phillipps, 1926b: 293, 1927a: 13, 1940: 15; Stokell, 1949: 492.

Galaxias reticulatus Richardson, 1848: 76 (syntypes (3): BMNH 1967.8.14.12–14, not seen; locality: Auckland Islands?).

Galaxias brocchus Richardson, 1848: 76 (holotype: BMNH 1855.9.19.800, not seen; locality: Auckland Islands?).

Galaxias argenteus: Whitley and Phillipps, 1940: 230 (partim).

Diagnosis. Differs from *G. argenteus* (Gmelin) (Fig. 4) in characters discussed in the diagnosis of that species (p. 353); differs from *G. postvectis* Clarke (Fig. 9) in coloration, in the absence of pyloric caeca and the presence of better-developed canine teeth in the jaws, in its longer and more slender head, and in its longer jaws, particularly the lower jaw. *G. postvectis* has somewhat fewer anal fin rays and branchiostegals, and more vertebrae and gill rakers.

Taxonomy. Two names that Stokell (1949) failed to apply to any New Zealand galaxiids are *G. brocchus* Richardson and *G. reticulatus* Richardson, described from
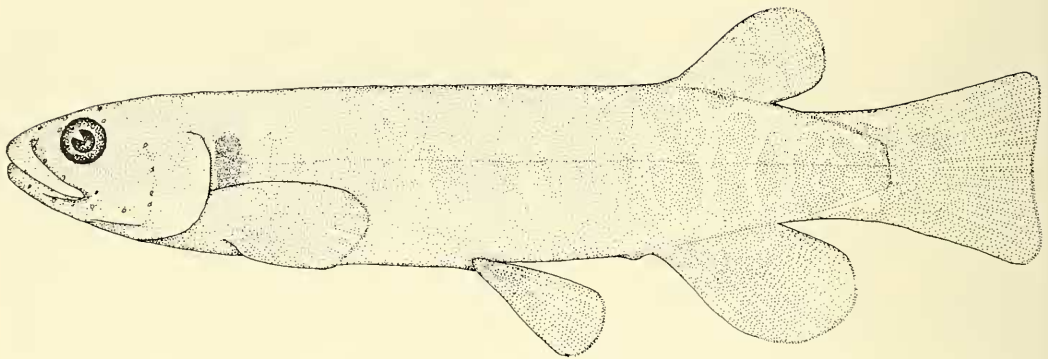
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* From P. 345.

Figure 6.   *Galaxias fasciatus* Gray, 155 mm L.C.F., Makahika Stream, Ohau River System.

the Auckland Islands. They were treated as synonyms of *G. fasciatus* by both Günther (1866: 209) and Regan (1905: 374). Fishes of this type have not otherwise been recorded from the sub-Antarctic islands of New Zealand, the only species there being *G. brevipinnis* Günther. Both Günther and Regan based their identifications on re-examination of Richardson's material, and the excellent likenesses of *G. fasciatus* in Richardson's figures (his plates 42 and 43) definitely support the view of Günther and Regan. Despite several collections from these islands (e.g., the Cape Expedition, 1941–45, see Stokell, 1950), *G. fasciatus* has not been re-collected there, and there is no evidence to suggest it is present. It is possible that it has become extinct in the islands since Richardson's fishes were collected, or that the material he studied was incorrectly labeled. Since *G. fasciatus* has marine larvae and juveniles, its dispersal to the sub-Antarctic islands is comprehensible, although its temperature preferences appear to be higher than those of *G. brevipinnis* (McDowall, 1965a: 299), indicating that these islands are probably less suited to *G. fasciatus* than to *G. brevipinnis*, which is present there. The possibility that the specimens were incorrectly labeled remains nothing more than a possibility. Nevertheless, *G. brocchus* and *G. reticulatus* are probably best regarded as synonyms of *G. fasciatus*, and as not occurring

on the sub-Antarctic islands of New Zealand, until further collections indicate otherwise.

Description. Stout bodied, trunk squarish to rounded in section, somewhat flattened dorsally with middorsal furrow present; trunk deep, greatest body depth at or a little in front of pelvic fins, depressed anteriorly on head and much compressed on caudal peduncle, which is short and about as deep as long. Lateral line a distinct lateral groove; accessory lateral line present. Head prominent, broader than deep and somewhat depressed; eye large, towards upper head profile, interorbital convex, very broad. Jaws about equal, lips prominent; cleft of mouth reaching beyond middle of eye, oblique. Profile of lower jaw from ventral aspect deep and narrow, U-shaped. Canine teeth strongly developed laterally in both jaws, mesopterygoidal teeth well developed; gill rakers well developed; pyloric caeca lacking.

Median fins well developed, with thick fleshy bases; prominent, greatest fin length much greater than base length, distal margin of fin much rounded; anal origin about below dorsal origin. Pectoral fin prominent and fleshy, rounded in outline; insertion moderately low. Pelvic fin expansive and long, inserted behind mid-point of standard length. Caudal fin fleshy, long, emarginate or truncated, emargination usually becom-
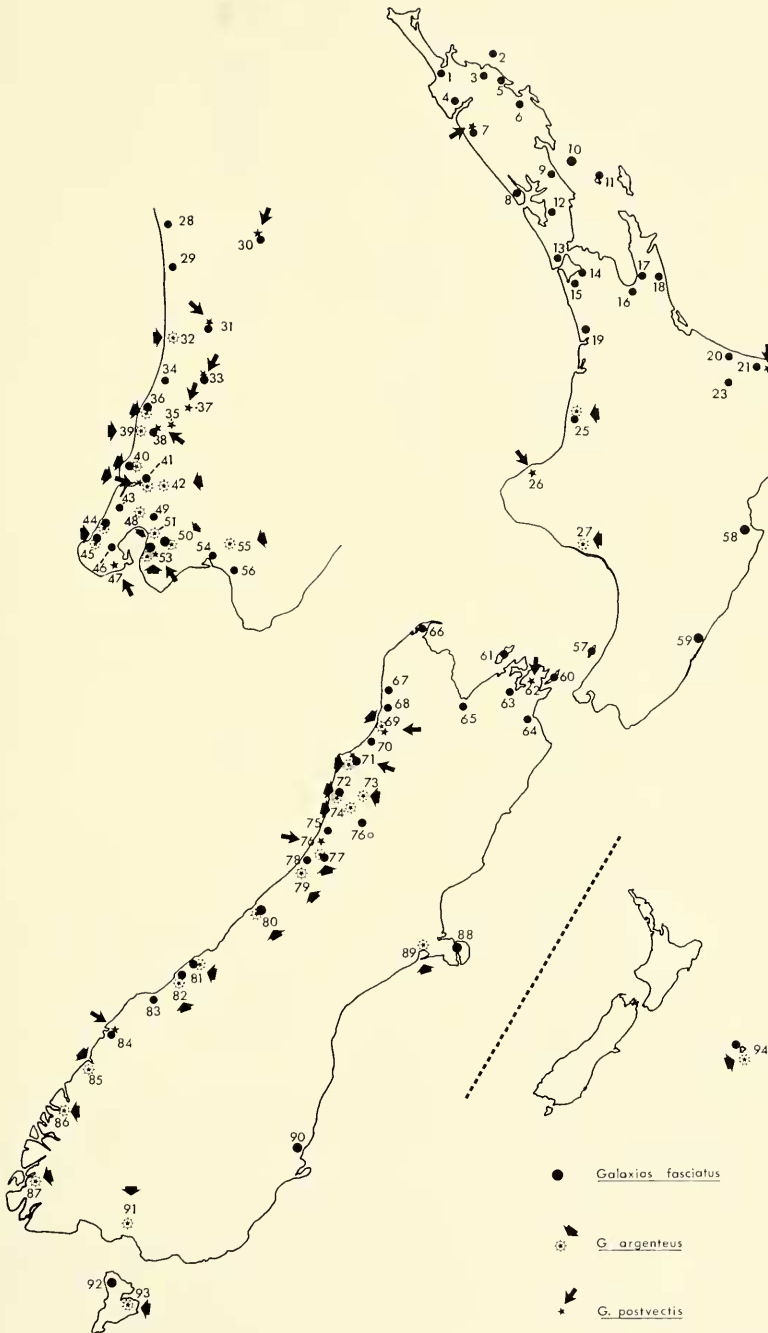
Figure 7.   Distribution of *Galaxias argenteus, G. fasciatus,* and *G. postvectis* (numbers in figure as in text pp. 355, 360, and 363).

TABLE 1. MORPHOMETRIC VARIATION IN LARGE, STOUT-BODIED SPECIES (FIGURES GIVEN AS PERCENTAGES OF DENOMINATOR OF RATIO).

	G. argenteus			G. fasciatus			G. postvectis		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	83.3	85.5	87.0	82.6	85.5	87.7	84.0	87.0	88.5
B.D.V./S.L.	18.7	21.0	23.4	15.0	17.9	21.4	16.4	19.6	22.4
L.C.P./S.L.	9.8	11.4	13.5	10.8	12.0	14.9	12.1	13.2	14.4
D.C.P./L.C.P.	100.0	113.6	125.0	61.0	76.9	114.9	95.2	102.0	113.6
Pre D./S.L.	74.6	76.3	77.5	73.0	76.5	79.4	70.9	74.1	76.9
Pre D./Pre A.	94.3	98.0	102.0	96.2	100.0	102.0	92.6	97.1	100.0
D.F.B./S.L.	9.4	11.9	13.4	9.5	10.8	11.9	10.2	11.3	11.6
D.F.B./D.F.M.	45.7	55.6	68.5	47.6	54.6	64.1	50.0	58.1	65.4
A.F.B./S.L.	13.5	15.4	17.8	11.9	14.0	16.1	11.1	13.4	14.4
A.F.B./A.F.M.	55.3	61.7	76.3	54.4	61.4	70.4	53.8	61.7	66.2
Pre Pel./S.L.	53.5	56.4	58.1	48.8	53.2	56.8	50.3	52.9	56.2
Pec.Pel./S.L.	26.8	29.1	31.3	26.8	29.4	32.7	28.9	31.8	35.3
Pec./Pec.Pel.	48.2	60.7	68.5	50.6	60.5	72.4	41.3	53.1	67.3
Pel.An./S.L.	20.8	22.7	25.0	21.4	24.1	27.4	23.1	24.8	26.5
Pel./Pel.An.	56.8	68.5	77.8	58.5	69.2	81.0	53.7	61.7	71.0
H.L./S.L.	27.0	29.1	30.5	22.8	25.9	28.6	21.2	23.0	25.0
H.D./H.L.	50.0	54.6	61.0	46.1	53.5	60.2	56.2	64.1	72.5
H.W./H.L.	57.5	64.9	74.1	55.9	71.4	78.1	59.5	70.4	78.1
Sn.L./H.L.	26.6	29.6	32.4	28.2	31.8	35.0	31.3	33.6	37.2
P.O.H.L./H.L.	50.8	55.6	61.4	45.7	50.5	55.0	49.0	50.8	54.1
Io.W./H.L.	40.0	42.5	46.1	40.3	43.9	47.4	40.5	44.8	47.4
D.E./H.L.	14.8	17.7	22.2	16.7	20.2	24.5	17.8	19.9	23.5
L.U.J./H.L.	41.2	43.7	45.7	42.4	48.5	51.8	37.5	40.7	43.3
L.M./H.L.	37.7	41.3	43.9	40.8	45.5	50.0	27.5	33.0	35.7
W.G./H.L.	33.7	37.3	42.4	33.3	40.8	46.5	34.4	38.8	42.6
Fish examined		36			60			25	

ing reduced with growth; fin depth usually somewhat less than greatest body depth; caudal peduncle showing considerable development of flanges.

Variation. Meristic: dorsal 9 (15), 10 (47), 11 (13), 12 (2), 13 (2); caudal 15 (1), 16 (60), 17 (2); anal 11 (3), 12 (29), 13 (42), 14 (10), 15 (1); pelvic 7 (63); pectoral 12 (20), 13 (47), 14 (7), 15 (4); branchiostegals 6 (3), 7 (18), 8 (40), 9 (3); vertebrae 56 (1), 57 (11), 58 (22), 59 (26), 60 (2), 61 (1); gill rakers 4–8 (1), 4–9 (5), 4–10 (3), 4–11 (3), 5–9 (5), 5–10 (19), 5–11 (1), 5–12 (1). Morphometric: see Table 1.

Coloration. Trunk color a dark purplish gray, banded dorsally and laterally with a series of narrow, pale, vertical bands. The bands are numerous in young fish, becoming narrower and more restricted to the posterior of the trunk as the fish grow.

Lateroventrally, the trunk coloration alters quite abruptly to a dull purplish brown. There is a prominent, dark, blue-black blotch above and behind the pectoral fin base. Frequently living in small, bush-covered creeks and streams, *G. fasciatus* appears well adapted to broken lighting conditions.

Size. *G. fasciatus* is one of the largest species of *Galaxias* and is known to grow to 260 mm. It commonly reaches 200 mm.

Population differences. Regional character differences were not found in diadromous populations of *G. fasciatus* from widely separated localities, although more intensive studies may show that they do occur.

Taxonomically interesting differences between diadromous and lacustrine populations were found. The fishes from Lake Okataina and the Kaihoka Lakes were
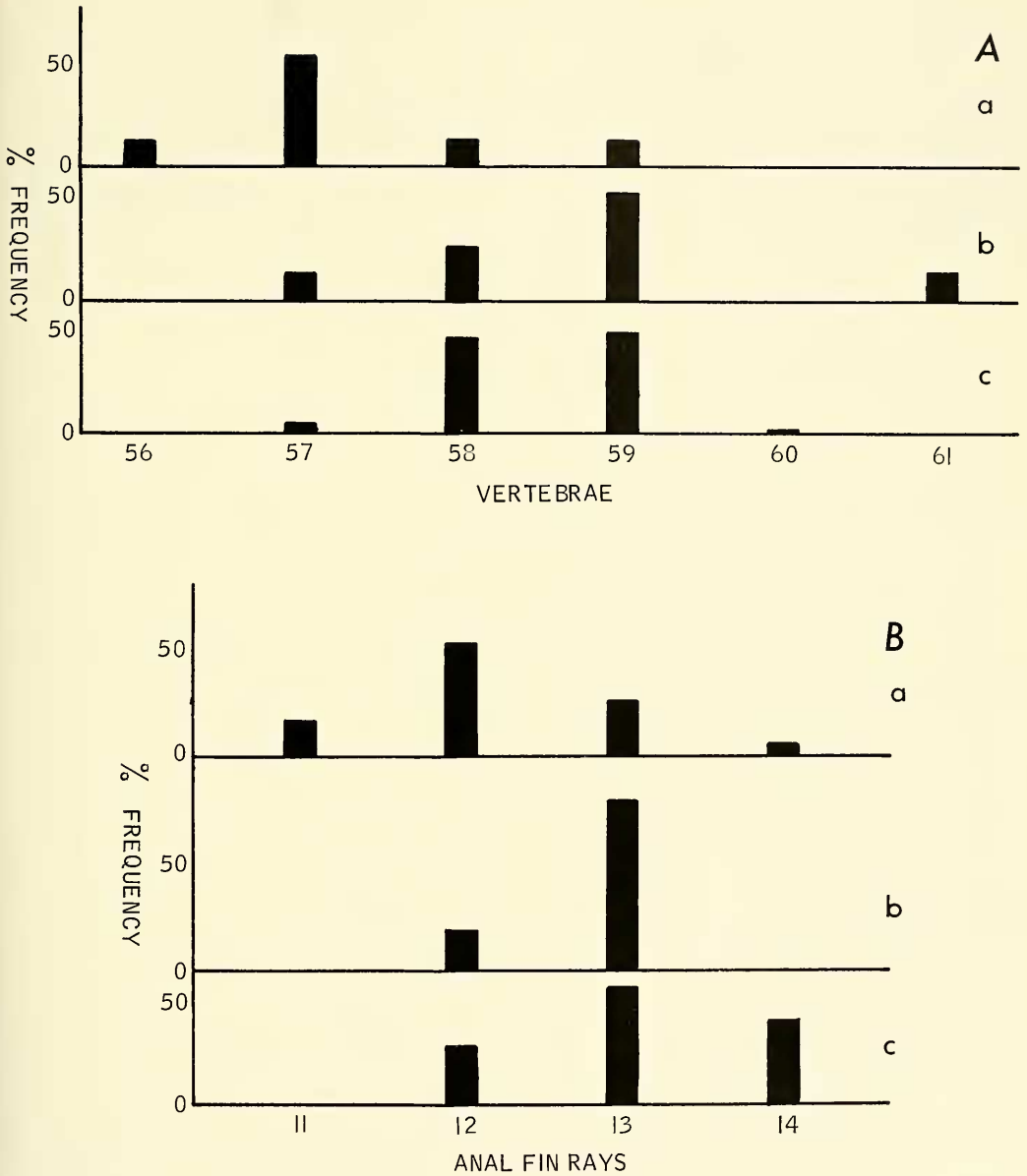
Figure 8. Variation in meristics in *Galaxias fasciatus*. A, Vertebrae; B, Anal fin rays; a, Lake Okataina (8 examples); b, Kaihoka Lakes (8 examples); c, Diadramous populations (47 examples).

found to be considerably more slender than sea-going fishes, and those in the Kaihoka Lakes had a shorter head (mean H.L./S.L. 25.9 in diadromous and 24.3 in Kaihoka populations). Lake Okataina ex- amples had fewer vertebrae and fewer rays in the anal fin (Fig. 8), although overlap with diadromous fishes was sub- stantial. Fewer branchiostegals were pres- ent in the fishes from the Kaihoka Lakes,

again with overlap (mean number, Kaihoka 6.75, diadromous 7.83).

As such landlocked populations become better understood, it may become necessary to recognize them as separate taxa at the species or subspecies level, as has been done with *G. maculatus*, but existing data do not justify this.

Habitat. *G. fasciatus* is essentially a lowland species, although it shows moderate penetration of river systems, even where substantial falls are present. Adults have been collected from small pools on the faces of high waterfalls and the juveniles are known to be able to climb wet, smooth surfaces with ease and rapidity. The locality furthest from the sea where *G. fasciatus* is known is the Kahuterawa Stream, a tributary of the Manawatu River about 40 miles upstream from the sea (C. L. Hopkins, pers. comm.). *G. fasciatus* is found mostly in small, quiet, winding creeks in coastal and lowland bush, usually hiding beneath cover such as logs, overhanging banks, tree roots etc., or amongst rock aggregations at the bases of small pools and cascades in the streams. This species is also quite common in the tannin-stained waters of flax swamps on the west coast of the South Island. Sea-going populations occur in Lakes Ianthe and Mapourika, in addition to the previously mentioned landlocked populations.

Life history. The breeding site of *G. fasciatus* is undescribed, but since ripe adults were collected in typical adult habitat, it seems unlikely that there is an adult breeding migration. Ripe males were collected with milt running as early as the end of February and study of gonad maturity suggests that breeding takes place mostly during the autumn and early winter (February to May or June). The eggs are of moderate size, 1.3–1.6 mm in diameter, and numerous; a female 160 mm long contained 5,100 eggs. The larvae are apparently carried to sea after hatching, and a subsequent upstream migration of the juveniles occurs the following spring, together with the whitebait of other diadromous species, although relatively late in the overall migration period (McDowall, 1965a). At migration the young *G. fasciatus* are transparent, little pigmented (Fig. 41), and measure 38–48 mm. Trunk pigmentation develops quickly after the fish enter fresh water, beginning as a general covering of melanophores; later a series of narrow, alternating light and dark bands develops. The slender juveniles become much stouter and the banding bolder, as the number of bands along the trunk increases. Eventually they extend over the dorsum of the trunk, where they form a reticulum of lighter markings on the more intense trunk coloration. With increasing size, the banding decreases in boldness and finally becomes obliterated along the anterior two-thirds of the trunk, especially in very large adults.

Distribution. The range of *G. fasciatus* is very extensive, especially on the western coasts of New Zealand. It is known from the following localities: Awanui River (Fig. 7: 1); Cavalli Islands (2); Kerikeri River (3); Mangamuka Stream (4*); Wainui River, tributary of the Orouaiti River (5); a stream at Waiomio (6); Merowhanara Stream, Waipoua System (7*); tributary of the Wairoa River at Tangaihi (8); tributaries of the Hakaru River at Mangawai (9); Chicken Islands (10, Stokell, 1949: 493); Little Barrier Island (11); Makarau River (12); a stream at Atkinson's Park, Titirangi (13); Whangamarino Stream (14); Mauku Stream (15); Waihou River (16, ? = Thames River, type locality); tributary of Kauaeranga River (17); Tairua River (18*); Waimai Stream (19); Pikowai Stream (20); Whakatane River (21); Lake Okataina (23*); Whanarua Stream (24*); Mokau River (25); Rangitikei River (28); Manawatu River (29); Kahuterawa Stream (30); Makahika Stream, Ohau System (31*); tributary of Otaki River at Otaki Forks (33*); Mangaone Stream, Te Horo (34); Waikanae River (36); Whareroa Stream (38*); Horo-
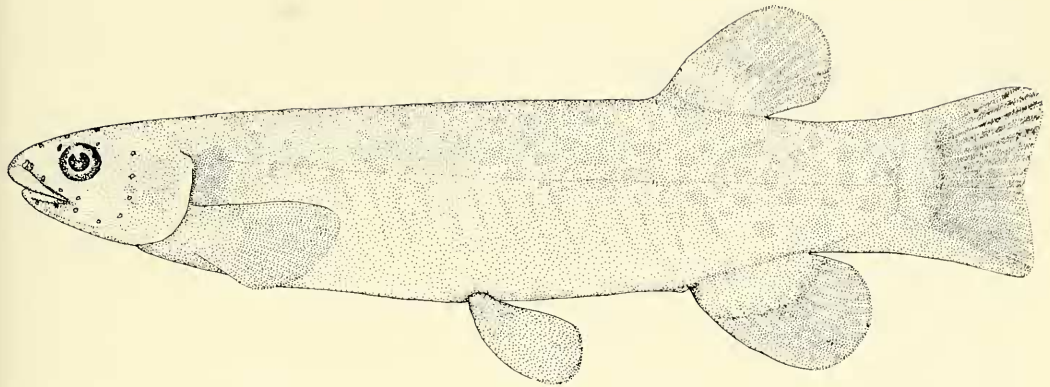
Figure 9. *Galaxias postvectis* Clarke, 178 mm L.C.F., stream at Otaki Forks, Otaki River System.

kiri Stream (40); Little Waitangi Stream (41); Tawa Stream (43); Makara Stream (45*), Hawkin's Gully Stream, a Makara tributary (44*); Kaiwharawhara Stream (46); Hutt River (49); Catchpool Stream, Wainuiomata System (50); Day's Bay Stream (53*); tributary of Lake Onoke (54); Whangamoana Stream (56*); Kapiti Island (57); Ngaruroro River (58); Pongoroa River (59); Arapawa Island (60); D'Urville Island (61); Momorangi Bay Stream (63*); Wairau River (64); "Nelson" (65, Stokell, 1949: 493); Kaihoka Lakes (66*); Karamea River (67); Little Wanganui River (68); Ngakawau River (70); Buller River (71); Grey River (72); Hokitika River (75); Taramakau River (76); Lake Ianthe (77*); Wanganui River (78); Lake Mapourika and Whataroa River (80*); Lake Paringa (81); Moeraki River (82); Jackson Bay Stream (83*); Awarua River (84); Waitati River (90*); Banks Peninsula (88); Stewart Island (92, Stokell, 1949: 493); Chatham Islands (94, Skrzynski, 1967: 95).

These localities show that *G. fasciatus* occurs commonly in western areas, and in the east in the North Auckland—Bay of Plenty districts. The general absence of the species from the east coast is probably the result of a combination of little suitable habitat and the fewer collections made, especially along the east coast of the North

Island. No localities are known to me from Southland and this is probably also due to the lack of collection.

Galaxias postvectis Clarke, 1899
Figure 9

Galaxias postvectis Clarke, 1899: 88 (holotype: unknown; locality: "western slopes," South Island); Stokell, 1960: 237.
Galaxias fasciatus: Regan, 1905: 374 (partim).
Galaxias charlottae Whitley and Phillipps, 1940: 230 (holotype: DMNZ 981, seen; locality: Queen Charlotte Sound).
Galaxias argenteus: Whitley and Phillipps, 1940: 231 (partim).

Diagnosis: G. *postvectis* differs from G. *argenteus* (Gmelin) (Fig. 4) and G. *fasciatus* Gray (Fig. 6) in characters noted in the diagnoses of these species (pp. 353 and 355 respectively).

Description. Stout bodied, trunk rounded in section, not flattened dorsally, with no middorsal groove, rather turgid-looking. Trunk deeper than broad, depressed anteriorly on head, which is not much flattened dorsally, compressed on caudal peduncle, which is short and deep, depth about equal to length. Lateral line an indistinct midlateral furrow; accessory lateral line present. Head prominent, a little broader than deep. Eye large, moderately deep set, interorbital convex, very broad. Jaws well developed, lower much shorter than upper, cleft reaching to about anterior

third of eye, oblique. Profile of lower jaw from ventral aspect rather deep and narrow, U-shaped. Canine teeth poorly developed in jaws, or lacking; mesopterygoidal teeth moderately developed; gill rakers and pyloric caeca moderately long.

Unpaired fins well developed with thick, fleshy bases, greatest fin length much greater than basal length; anal origin a little behind dorsal origin. Pectoral fin well developed, inserted moderately high, somewhat triangular in shape, with longest rays near upper margin. Pelvic fins long and expansive, inserted behind midpoint of standard length. Caudal fin rather fleshy, moderately long, emarginate, tending towards truncation in very large individuals, fin depth a little less than greatest body depth; caudal peduncle flanges well developed.

Variation. Meristic: dorsal 9 (6), 10 (15), 11 (4); caudal 16 (25); anal 10 (1), 11 (10), 12 (14); pelvic 7 (25); pectoral 13 (2), 14 (14), 15 (9); branchiostegals 6 (2), 7 (21), 8 (2); vertebrae 59 (5), 60 (8), 61 (8), 62 (1); gill rakers 4–12 (1), 5–11 (3), 5–12 (1), 5–13 (2), 6–11 (10), 6–12 (5), 6–13 (2), 7–12 (1). Morphometric: see Table 1, p. 358.

Coloration. Usual body color a deep brownish blue, with paler, indistinct, irregular marbling of slightly darker shade on the dorsal and dorsolateral trunk, and extending on to the lateral and lateroventral trunk or resolving into faint, slightly oblique bands. A purplish blotch is present above the pectoral fin base. Ventrally, the trunk is paler, more brownish in color, but nevertheless intensely pigmented. In transmitted light the fin bases appear a rufous color. Between the fin rays on the distal two-thirds to half of the median fins, there is bold and distinctive brown-black banding, which fades as the fleshiness of the fin bases develops.

Size. The largest individual examined measured 250 mm, but Stokell (1960: 238) listed one at 261 mm. Individuals 180–200 mm long were relatively abundant.

Population differences. Insufficient large samples were available to enable meaningful comparison of samples from different localities.

Habitat. G. *postvectis* is almost always collected from small, heavily bush-covered streams that are unmodified by agricultural development. These streams are usually stable, with small pools, often overhung with tree roots, or containing fallen trees. Logs in the streams often form small pools and cascades, and G. *postvectis* occurs in these. It is probably very sensitive to removal of bush cover and stream modification.

Life history. The life history pattern of G. *postvectis* is similar to that of the other stout-bodied species. The eggs appear to be relatively small, although the only ripe individuals examined were somewhat dehydrated, preventing satisfactory measurement of the eggs. In these fishes, the eggs were 1.0–1.5 mm diameter. A female 205 mm long contained about 13,000 eggs. The breeding site is undiscovered, but is likely to be close to the normal adult habitat. The larvae are apparently carried downstream to the sea, and develop and grow in the sea during the winter. The upstream migration of the whitebait juveniles occurs concurrently with the other species, although probably towards the end of the migration period, along with G. *fasciatus* and G. *argenteus*. Adults collected from the Ohau River system in February showed gonads to be at an early stage of maturation; one fish from the Mangaone Stream, taken in late May, and another from the Waikanae River in early June had ova about ripe. Further examples collected from the Waikanae River in early September were spent or in early stages of gonad rejuvenation. Thus spawning probably occurs in autumn or early winter.

The transparent whitebait of G. *postvectis* (Fig. 44) develop a covering of melanophores soon after entering fresh water, but do not develop pale bands like the young of G. *fasciatus* and G. *argenteus*.
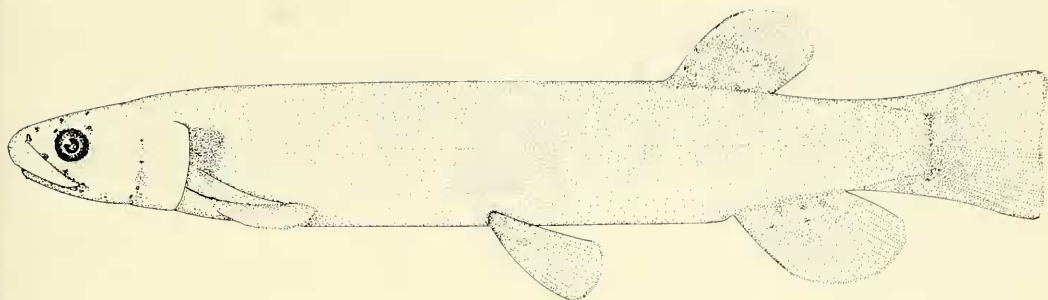
Figure 10. *Galaxias brevipinnis* Günther, 185 mm L.C.F., stream at Erua, Upper Wanganui River System.

Dusky brown bands develop along the sides of the trunk as the fishes grow and attain the stout-bodied form of the adult.

Distribution. Like the other species with marine juveniles, *G. postvectis* is rather widely distributed in New Zealand. Collection localities are few, even though they extend along the west coast of New Zealand from the Waipoua Kauri forests in North Auckland to the Awarua River, Big Bay, in the south. Localities in the Bay of Plenty and the Marlborough Sounds are also known. As yet, *G. postvectis* has not been recorded from the east coast between East Cape and Southland. This probably represents a real distributional gap for much of the Canterbury area, but *G. postvectis* seems likely to be found in some Southland streams and on Banks Peninsula, where overgrown bush streams with stable, rocky beds are present. Very little collection has been done on the east coast of the North Island, and *G. postvectis* may also be found to occur there. It is presently known from the following localities: Merowhanara Stream (Fig. 7: 7*); Waimana River (22); Ratapiko (26); Kahuterawa Stream, Manawatu System (30); Makahika Stream, Ohau System (31*); a stream at Otaki Forks, Otaki River (33*); Waikanae River and its tributaries, the Mangakotukutuku (35*) and Ngatiawa Streams (37*); Whareroa Stream (38); Little Waitangi Stream (42); Day's Bay Stream (53); Owhiro Bay Stream (47*); Queen Charlotte Sound (62, Whitley and Phillipps,

1940: 230); Mokihinui River (69); Buller River (71); Waimea River (76*); Awarua River (84).

Galaxias brevipinnis Günther, 1866
Figure 10

Galaxias brevipinnis Günther, 1866: 213 (syntypes (3): BMNH 1853.2.14.5–7, not seen; locality: New Zealand); Hutton, 1872: 59, 1896: 317, 1904: 51; Regan, 1905: 374; Waite, 1909: 586; Rendahl, 1926: 2; Phillipps 1927a: 13, 1940: 21; Stokell, 1954: 415, 1960: 236.

Galaxias olidus: Hutton, 1872: 270 (not *G. olidus* Günther, 1866: 209).

Galaxias campbelli Sauvage, 1880: 229 (syntypes (4): MNHNP A-2381, not seen; locality: Campbell Island); Stokell, 1949: 487, 1950: 8.

Galaxias lynx Hutton, 1896: 317 (holotype: CMCNZ 70 seen, paratypes: CMCNZ 71 (3) seen, AMS 1B-435–6 (2) not seen; locality: Lakes Coleridge and Wakatipu); Stokell, 1949: 486.

Galaxias robinsonii Clarke, 1899: 89 (holotype: unknown; locality: western slopes, South Island); Phillipps, 1926a: 98.

Galaxias bollansi Hutton, 1901: 198 (holotype: BMNH 1905.11.30.23, not seen; locality: Auckland Islands).

Galaxias huttoni Regan, 1905: 373 (syntypes (7): 1905.11.30.27–33, seen; locality: "Lake Rainiera," an unknown New Zealand place name); Phillipps, 1924b: 190.

Galaxias castlae Whitley and Phillipps, 1940: 229 (holotype: DMNZ 2070, seen; locality: Lake Waikaremoana).

Galaxias koaro Phillipps, 1940: 35 (holotype: unknown; locality: Lakes Rotoaira and Rotopounamu); Stokell, 1949: 487.

Diagnosis. Differs from *G. vulgaris* Stokell (Fig. 16) in having more vertebrae (especially in the south, where the two

species are sympatric) and somewhat higher fin ray counts in the dorsal, anal, and pectoral fins. The gill rakers are much better developed in *G. brevipinnis* than in *G. vulgaris*, and the lower jaw recedes further in the former species. *G. brevipinnis* breeds in the autumn and has migratory marine or lacustrine whitebait juveniles; in contrast, *G. vulgaris* breeds mostly in the spring and has no migratory juvenile.

Taxonomy. Nine nominal species of the *G. brevipinnis* type have been described. Stokell (1949: 486–490, 1954: 413, 1960: 236) reduced the number recognized to three, viz. *G. brevipinnis* Günther, *G. lynx* Hutton, and *G. koaro* Phillipps. Examination of many large samples from a great variety of localities has shown that these populations represent a single, variable species.

From the description of Regan (1905: 377), there appears to be little, if any, difference between *G. brevipinnis* and *G. weedoni* Johnston. In *G. weedoni*, Regan recorded canine teeth in the jaws, the cleft of the jaw extending below the eye, long, low-placed pectoral fins, a long, slender caudal peduncle, and a blue-black blotch above the pectoral fin base. Meristic data— vertebrae 57–60, dorsal fin rays 10–11, anal rays 10–12, pectoral rays 14–15, branchiostegals 8–9—are all consistent with the inclusion of *G. weedoni* in *G. brevipinnis*. I have seen only juveniles of *G. weedoni*, but their coloration is identical with that of juvenile *G. brevipinnis* and different from that of any other galaxiid I have seen. And they are long and slender, have a much shortened lower jaw, and have the anal fin set back below the middle of the dorsal, just as in *G. brevipinnis*. Accordingly, I think that the two species are conspecific, although formal synonymy of *G. weedoni* in *G. brevipinnis* must await examination of adult specimens.

Description. Elongate and slender-bodied, trunk rounded in section, somewhat flattened dorsally, with slight development of middorsal furrow; trunk much depressed anteriorly on head, compressed behind vent; dorsal and ventral trunk profiles about parallel. Caudal peduncle moderately long and slender, substantially longer than deep. Lateral line a somewhat indistinct lateral crease; accessory lateral line present. Head moderately long, much broader than deep, cheeks broadening below eye; jaws long, lower markedly shorter than upper and tucked behind it when mouth is closed, lips prominent. Snout short. Cleft of mouth slightly oblique, extending to about middle of eye, profile of lower jaw from ventral aspect deep and rather narrow, U-shaped, but gape broad in head length. Eye rather small, deep on lateral head, interorbital convex. Jaws with prominent canines laterally; mesopterygoidal teeth moderately well developed; gill rakers and pyloric caeca well developed.

Fins well developed, thick and fleshy; dorsal and anal short based but extending back well beyond bases, distal margins much rounded; anal origin usually well behind dorsal origin. Pectoral fin expansive, inserted low latero-ventrally, with lamina of fin directed ventrally; pelvic-anal interval rather short, fin expansive and long, inserted at about midpoint of standard length. Caudal fin truncated to slightly emarginate, fin tips somewhat rounded, depth about equal to body depth; peduncle flanges weakly to moderately developed.

Variation. Meristic: dorsal 9 (30), 10 (126), 11 (54), 12 (7); caudal 15 (5), 16 (206), 17 (3), 18 (1); anal 9 (3), 10 (21), 11 (113), 12 (61), 13 (18); pelvic 6 (4), 7 (201), 8 (12); pectoral 13 (4), 14 (50), 15 (113), 16 (48), 17 (2); branchiostegals 6 (1), 7 (54), 8 (125), 9 (36); vertebrae 52 (1), 53 (2), 54 (9), 55 (16), 56 (30), 57 (45), 58 (36), 59 (53), 60 (77), 61 (63), 62 (16), 63 (5), 64 (2); gill rakers 3–9 (4), 3–10 (5), 4–8 (2), 4–9 (67), 4–10 (53), 4–11 (9), 4–12 (1), 5–8 (1), 5–9 (4), 5–10 (13), 5–11 (6), 5–12 (1), 6–11 (1). Morphometric: see Table 2, p. 365.

Coloration. Usually dark colored, the

Table 2. Morphometric variation in large, slender species (figures given as percentages of denominator of ratio).

	G. brevipinnis			G. vulgaris		
	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	84.8	87.0	89.3	84.0	87.0	89.3
B.D.V./S.L.	11.0	13.2	15.3	11.0	12.9	15.4
L.C.P./S.L.	11.8	13.1	15.8	11.9	14.1	16.5
D.C.P./L.C.P.	59.5	71.9	88.5	56.2	69.4	94.3
Pre D./S.L.	68.5	73.5	81.3	67.6	71.9	75.8
Pre D./Pre A.	90.9	95.2	99.0	90.1	95.2	100.0
D.F.B./S.L.	7.8	9.4	10.8	7.2	8.9	10.7
D.F.B./D.F.M.	47.6	56.8	70.9	47.6	56.5	64.5
A.F.B./S.L.	8.8	10.5	12.2	8.9	10.5	13.4
A.F.B./A.F.M.	50.0	61.7	73.0	51.0	61.4	74.1
Pre Pel./S.L.	46.3	52.2	57.8	49.3	53.0	56.5
Pec.Pel./S.L.	27.2	30.7	36.8	28.2	32.0	36.4
Pec./Pec.Pel.	43.1	55.6	68.3	36.8	49.6	61.5
Pel.An./S.L.	20.9	25.7	30.4	19.6	23.1	26.5
Pel./Pel.An.	44.4	58.9	77.4	43.2	57.7	72.7
H.L./S.L.	20.7	23.6	28.7	20.5	23.4	27.0
H.D./H.L.	41.7	49.3	55.9	45.9	52.6	59.9
H.W./H.L.	56.2	67.6	78.7	57.5	67.1	78.1
Sn.L./H.L.	26.3	30.7	34.4	26.7	31.6	36.2
P.O.H.L./H.L.	48.5	55.0	70.4	43.7	51.8	58.1
Io.W./H.L.	32.5	37.7	44.1	34.5	38.6	43.7
D.E./H.L.	13.9	17.8	25.0	14.8	17.6	22.0
L.U.J./H.L.	37.3	42.9	48.1	33.3	43.1	51.0
L.M./H.L.	32.4	38.5	43.7	33.3	38.5	47.2
W.G./H.L.	40.0	42.7	56.2	35.1	43.5	55.6
Fish examined		160			215	

basic body color a dark gray-brown, the dorsal and lateral trunk covered with irregular greenish brown to gold vermiculations, sometimes as a coarse, bold reticulum or varying to dense, fine speckling. Belly paler, a smokey gray. A prominent blue-black blotch is present above and behind the pectoral fin base.

Size. G. *brevipinnis* is one of the larger Galaxiidae, the largest examined by the writer being 220 mm long. An example described by Phillipps (1926a: 99) as *G. robinsonii* Clarke was 9.6 inches (240 mm) and one described by Clarke (1899: 99) 8.2 inches (213 mm) long. G. *brevipinnis* commonly grows to 160–185 mm.

Population differences. Populations of fishes belonging to G. *brevipinnis* are widespread in lakes and rivers throughout New Zealand, and examination of populations from too few and too isolated localities, together with the variability between these populations, led earlier workers to regard these series of populations as belonging to several species.

The most variable character, and the one chiefly used to justify several species, is vertebral number. Arranging the data from lake populations in north-south order, there is a cline in the number of vertebrae, with no justifiable division of the populations into two or more groups (Fig. 11). There are some irregularities in the cline, but overlap of data from adjacent populations is usually substantial. The more than 250 mile geographic break between the populations in Lake Taupo and the Nelson Lakes (Rotoiti and Rotoroa) coincides with the greatest break in the cline, but this is somewhat bridged by the more southern Lake Howard population.

The vertebral cline appears to be related
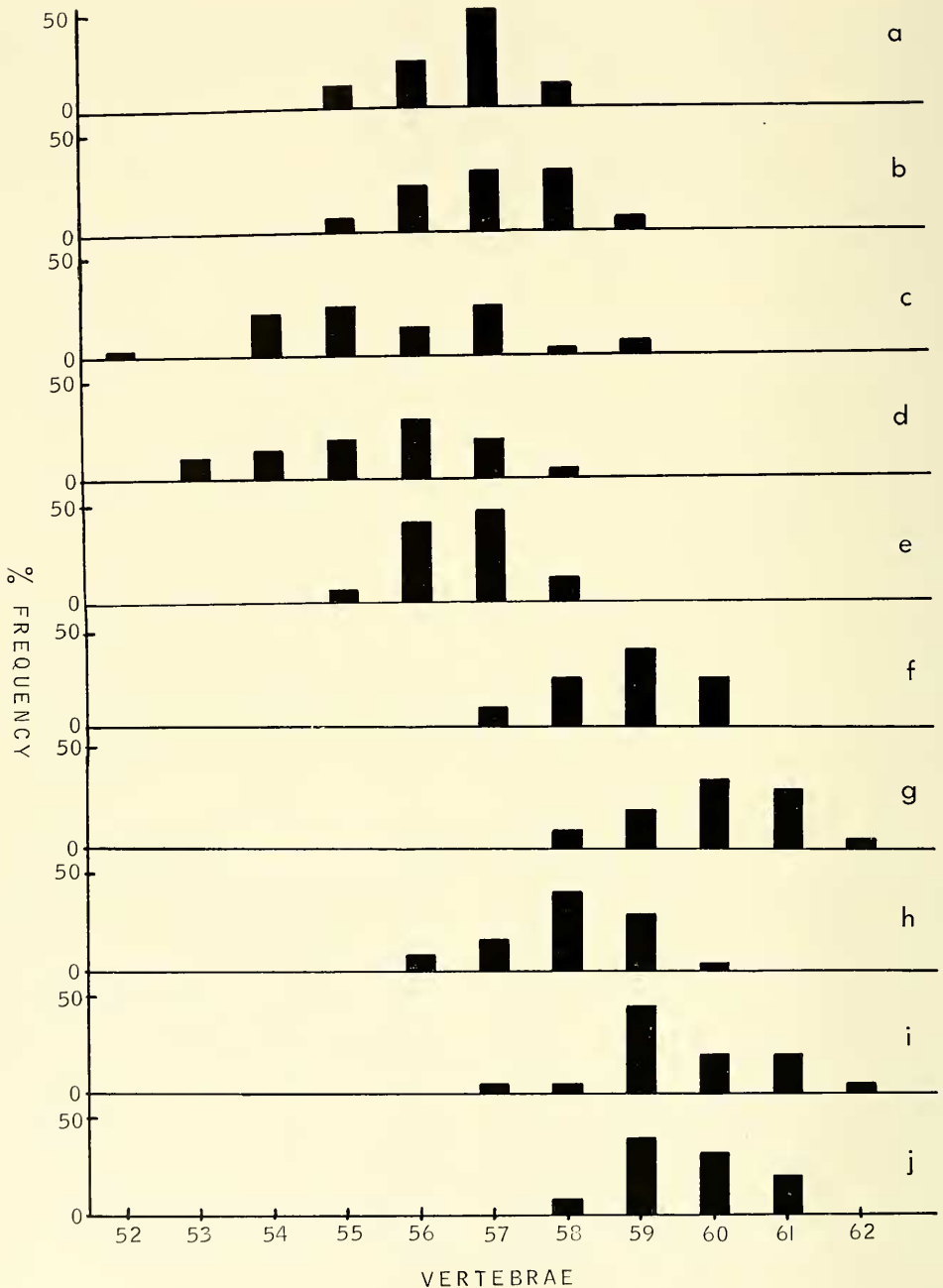
Figure 11. Variation in vertebral number in lacustrine *Galaxias brevipinnis* populations, in north-south series. a, Lake Ratorua (8 examples); b, Lake Okataina (25 examples); c, Lake Waikaremoana (27 examples); d, Lake Kiriopukae (20 examples); e, Lake Taupo (31 examples); f, Lakes Rotoroa-Rotoiti, Nelson Lakes (20 examples); g, Lake Sumner (20 examples); h, Lake Howard (25 examples); i, Lake Wanaka (20 examples); j, Lake Mahinerangi (25 examples).
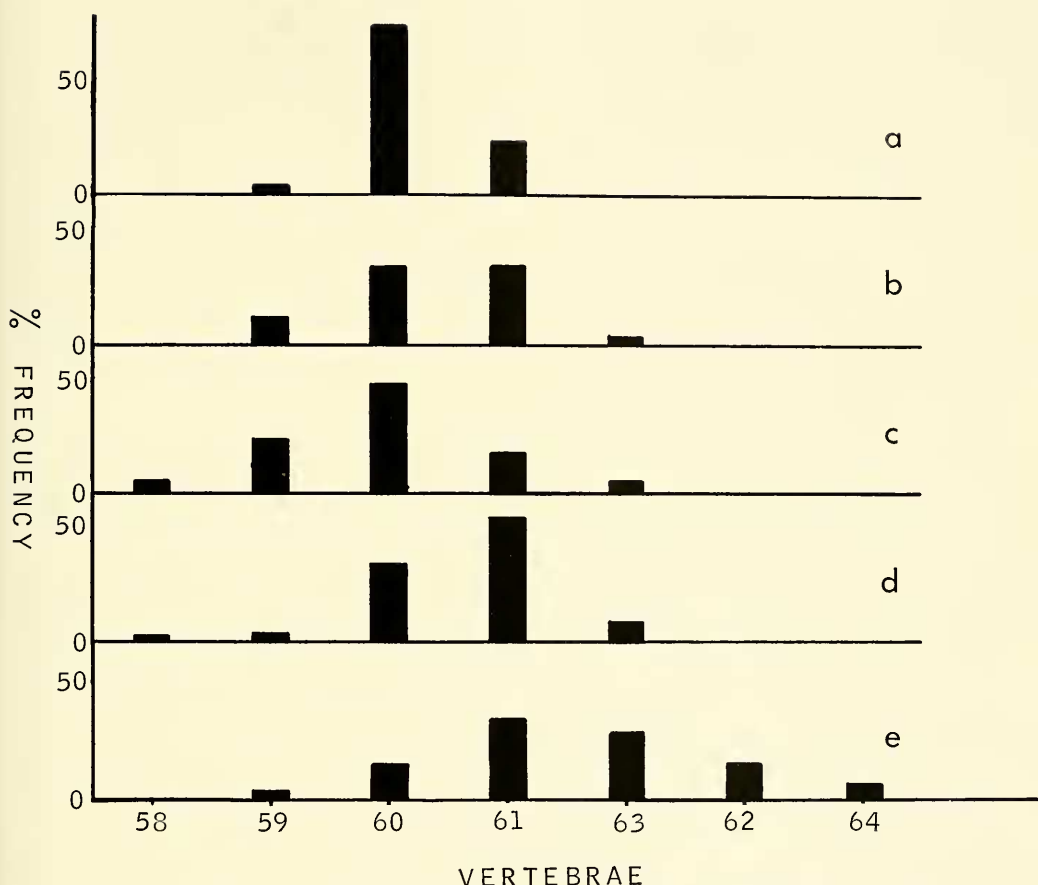
Figure 12. Variation in vertebral number in diadromous *Galaxias brevipinnis* populations. a, Northwestern North Island —North Auckland District (30 examples); b, Southern North Island—Wellington District (26 examples); c, Midwestern South Island (22 examples); d, Southwestern South Island—Haast District (36 examples); e, Sub-Antarctic Islands of New Zealand —Auckland and Campbell Islands (34 examples).

to temperatures, the number of vertebrae being lower in fishes from the more northern (warmer) lakes. Growth in these lakes is likely to be more rapid during critical developmental periods. Many workers (see Lindsey, 1961, for a recent summary) have noted the tendency for closely related species to have more parts (particularly vertebrae) towards the polar end of their range. If temperature is affecting vertebral number, then it is not a valid character for use in dividing the northern and southern population series into two species. Other meristic characters did not appear to ex-

hibit clinal variation and varied rather irregularly, but Lindsay has noted that clinal variation in one character does not necessarily correlate with variation in another character.

Sea-going specimens were found to have about the same number of vertebrae as lacustrine examples in the more southern lakes. They exhibited variation of similar extent to that seen in other species with marine whitebait. There is slight displacement towards greater vertebral number with increasingly southern location of populations (Fig. 12, cf. *G. argenteus*, Fig.
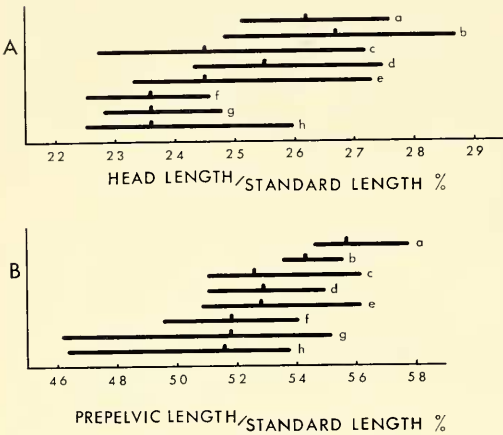
Figure 13. Variation in body proportions in lacustrine *Galaxias brevipinnis* populations. A, Head length/standard length ratio; B, Prepelvic length/standard length ratio; a, Lake Rotorua (7 examples); b, Lake Okataina (5 examples); c, Lake Waikaremoana (30 examples); d, Lake Kiriopukae (33 examples); e, Lake Taupo (18 examples); f, Lakes Rotoroa-Rotoiti, Nelson Lakes (20 examples); g, Lake Howard (21 examples); h, Lake Wanaka (20 examples).
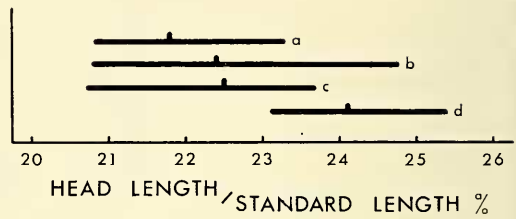

Figure 14. Variation in head length in diadromous *Galaxias brevipinnis* populations. a, Northwestern North Island —North Auckland District (9 examples); b, Southern North Island—Wellington District (23 examples); c, Western South Island (14 examples); d, Sub-Antarctic Islands of New Zealand—Auckland and Campbell Islands (21 examples).

5). The more disjunct sub-Antarctic island populations showed greater distinctness, as is predictable from their extremely southern position in the range of *G. brevipinnis.*

The most variable morphometric characters proved to be head length and prepelvic length. In lacustrine populations both head length/standard length and prepelvic length/standard length ratios exhibited north-south clinal variation, similar to that of vertebral number (Fig. 13). Variation in head length in diadromous populations showed a slight trend towards increase in length with southern displacement, again with the sub-Antarctic island populations standing somewhat apart from mainland populations (Fig. 14).

No other characters were found that distinguished any group of lake populations from any other, or the lake populations from diadromous populations. Although the inclusion of all these populations in *G. brevipinnis* results in a somewhat more variable species than some other New Zealand species of *Galaxias,* the alternative course results in two or more morpho-

logically similar forms that differ only in clinal characters. If recognized as distinct, such species would be much more similar to each other than any other closely related species pairs in the fauna.

This is similar to the case of the Northern Hemisphere salmonids in which euryhaline diadromous populations have become locally restricted to fresh water, either voluntarily, as Atlantic salmon, *Salmo salar,* have in the Manapouri-Te Anau system in New Zealand, or by the development of downstream barriers to migration. Bigelow and Schroeder (1963: 559), for instance, recorded *Osmerus eperlanus* from both coastal-estuarine situations and landlocked situations. In some cases, as in *S. trutta* in New Zealand, the diadromous and freshwater forms mingle and may form a single gene pool. This may also occur in *G. brevipinnis,* since few of the lacustrine populations are prevented from moving downstream and interbreeding with diadromous populations. In other instances, in the northern salmonoids and in *G. brevipinnis,* populations are found to be truly landlocked and thus completely isolated geographically.

Habitat. As presently defined, *G. brevipinnis* comprises forms inhabiting a variety of types of river and lake systems. Many diadromous populations are known in lowland streams, but they may migrate a great distance inland, e.g., into tributaries of the Wanganui River on the slopes of Mount

Ruapehu at altitudes approaching 3,000 feet (900 m) and streams on Mount Egmont at more than 4,000 feet (1,200 m) (G. C. Kelly, pers. comm.). Diadromous populations occur in a few lakes, e.g., Lakes Mapourika and Kaniere, the juveniles migrating from the sea into the lakes and finally living as adults in the lake tributaries. The possibility that both lacustrine and diadromous populations occur in such lakes as these cannot at present be excluded.

Most lake populations appear to be restricted largely to the lakes and their tributaries; the juveniles shoal in the lakes and the adults inhabit the lake tributaries but are mostly absent from the lakes themselves. A fluviatile habitat is to be expected for the adults, from their obviously depressed, benthic form, adapted to rapid waters, and from the very definite upstream migration of the juveniles. Lake Howard has no tributaries, and the adults are found in the lake amongst rocks near the shore, but this seems unusual. In a few cases, e.g., Lake Coleridge, it has been found that the lacustrine populations also invade the rivers below the lakes. Lacustrine populations vary greatly in altitude, from about 200 feet (60 m) in Lake Alice to in excess of 2,000 feet (610 m) in Lakes Waikaremoana, Rotoiti (Nelson Lakes), and Monk. However, most of the lakes lie between 600 and 1,500 feet (180–460 m).

Whether diadromous or lacustrine, the adults of *G. brevipinnis* are characteristically captured from small, cold, rapidly flowing, stable, rocky streams which are often heavily overgrown with bush. The fishes are very secretive and live hidden amongst boulders in the most swiftly flowing water. In streams unmodified by clearing of the forest and agricultural development, *G. brevipinnis* may form large and dense populations.

Formation of landlocked populations. Many of the landlocked populations of *G. brevipinnis* must post-date the last Pleisto-

cene glaciation. Fleming (1962: 89) showed that the lower limits of the ice cap in New Zealand during the last glaciation (about 15,000 years ago) would have completely engulfed many of the South Island upland lakes, in which *G. brevipinnis* is now present. Lake Mahinerangi is even more recent; Dollimore (1962: 345) reported that this lake was formed artificially as a hydro lake in 1911. Most of the lakes in the South Island occur in glacial valleys, and their formation resulted from the retreat of the ice and deposit of moraine (C. A. Fleming, pers. comm.); the now-resident fish populations must have entered the lakes since that time. If the lake populations are geographically isolated by landlocking from diadromous populations, their great morphological similarity to the diadromous form is due to the recency of their isolation. The thermal lakes are also recently formed, and their populations of *G. brevipinnis* are of very recent derivation, almost certainly post-glacial.

Life history. Little has been reported on the breeding of *G. brevipinnis*. The occurrence of a spring migration of juveniles suggests that, like other species with marine juveniles, spawning occurs predominantly in the autumn and early winter. Ripe and mature adults were most common in samples collected from March through May, although a single fully ripe female was found in a November sample. The eggs of *G. brevipinnis* are of moderate size and numerous, 1.3–1.6 mm diameter in a female 188 mm long and carrying about 7,500 eggs.

The spawning habitat has not been described, but localities from which ripe, strippable adults were collected were not different from usual adult habitats, suggesting that there may be little or no breeding migration.

On hatching, the larvae are apparently washed downstream into the sea (or lake) and develop there during the winter. The slender, transparent whitebait juveniles (Fig. 42) migrate upstream primarily dur-
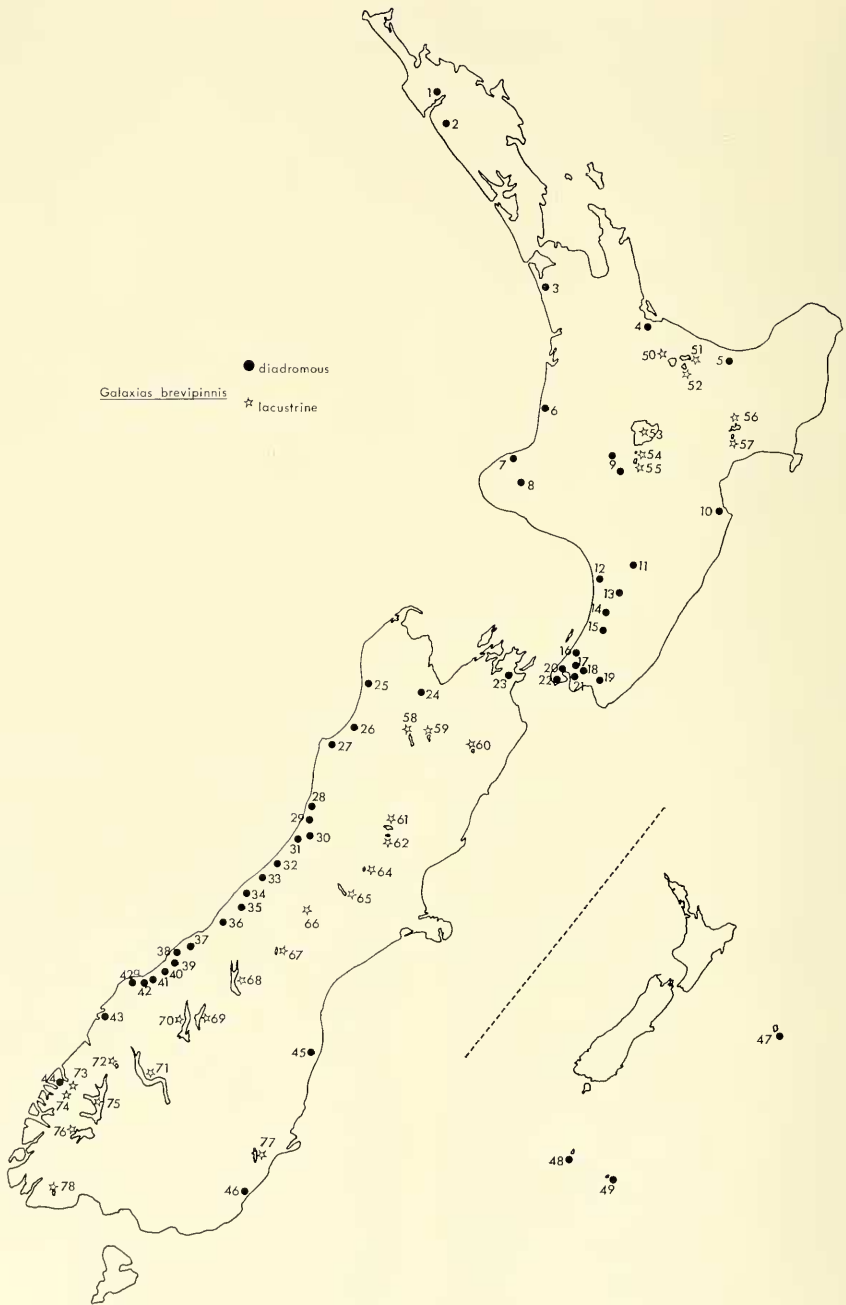
Figure 15. Distribution of *Galaxias brevipinnis* (numbers in figure as in text, p. 371).

ing the spring; in diadromous populations the migration occurs concurrently with that of other whitebait species, in huge, mixed-species shoals (McDowall, 1965a: 290), although probably early in the migration period.

The transparent fishes become pigmented soon after migration. Sub-adult coloration develops initially as an overall covering of melanophores. These become concentrated along the myotomes and develop into dark, vertical chevron-shaped bands, which subsequently become subdivided to form an irregular blotching pattern. This bold blotching may persist in the adult, or may become progressively more and more fragmented to produce the vermiculations found in most adults.

Distribution. G. *brevipinnis* is probably the most widely distributed species of *Galaxias* in the New Zealand region. If it is shown to be conspecific with G. *weedoni*, it has trans-Tasman distribution. Coastally it is widespread, though at present, few localities are known from the east coast between East Cape and Southland. It is very common on the west coast and also in upland lakes, especially east of the main divide in the South Island, and occurs on many islands, including the very remote Chatham, Auckland, and Campbell Islands.

As with the other diadromous species, inland range is somewhat limited by physical barriers in the rivers up which the fishes migrate, but this limitation affects G. *brevipinnis* less than other galaxiids on account of its exceptional climbing ability.

Populations believed to be diadromous are known from the following localities: Mangamuka Stream (Fig. 15: 1); Merowhanara Stream, Waipoua System (2*); Waikato River (3); Te Puna Stream (4*); Whakatane River (5); Mokau River (6); Waiwakaiho River (7); Patea River (8); tributaries of the Wanganui River near Erua (9*); Ngaruroro River (10); Rangitikei River (12); Pohangina River (11, Phillipps, 1926a: 98) and Kahuterawa Stream (13), Manawatu System; Makahika River,

Ohau System (14*); tributary of Otaki River at Otaki Forks (15*); Ngatiawa and Mangakotukutuku Streams, Waikanae System (16*); Horokiri Stream (17); Hutt River at Kaitoke (18); Kaiwharawhara Stream (20); Day's Bay Stream (21*); Lyall Bay and Owhiro Bay Streams (22); tributary of Lake Onoke (19); Wairau River (23); Pokororo River, Motueka System (24*); Karamea River (25); Ngakawau River (26); Buller River (27); Grey River (28); Taramakau River (29); Lake Kaniere (30); Hokitika River (31); Waitaha River (32); Wanganui River (33); Whataroa River (34); Lake Mapourika (35*); Cook River (36); Moeraki River (37); Waita River (38); Haast River (39*); Okuru and Turnbull Rivers (40); Waiatoto River (41); Arawata River (42); Jackson Bay Stream (42a*); Awarua River (43); Ethne River (44); Waitaki River (45); Clutha River (46); Chatham Islands (47, Skrzynski, 1967: 95); Campbell Island (48*); Auckland Islands (49*).

Lacustrine populations occur in the following lakes: Rotorua (50*); Rotoiti (51*); Okataina (52*); Taupo (53*); Rotopounamu (54); Rotoaira (55); Waikaremoana (56*); Kiriopukae (57*); Rotoroa (58*); Rotoiti (59*, Nelson Lakes); Bowscale Tarn (60); Sumner (61*); Taylor (62); Pearson (64, Stokell, 1949: 486); Coleridge (65*); Howard (66); Alexandrina (67); Ohau (68, Stokell, 1955: 23); Hawea (69); Wanaka (70*); Wakatipu (71); Hawdon (72, Stokell, 1949: 486); Alice and Marchant (73), and Katherine (74, all Cunningham, 1951: 74); Te Anau (75) and Manapouri (76, both Stokell, 1959a: 255); Mahinerangi (77*); Monk (78, Riney et al., 1959: 45).

The absence of lacustrine populations in the region between the southern end of the volcanic plateau and the Nelson Lakes is almost certainly attributable to the absence of upland lakes there. Otherwise, the distribution of lacustrine populations of G. *brevipinnis* is fairly continuous from the
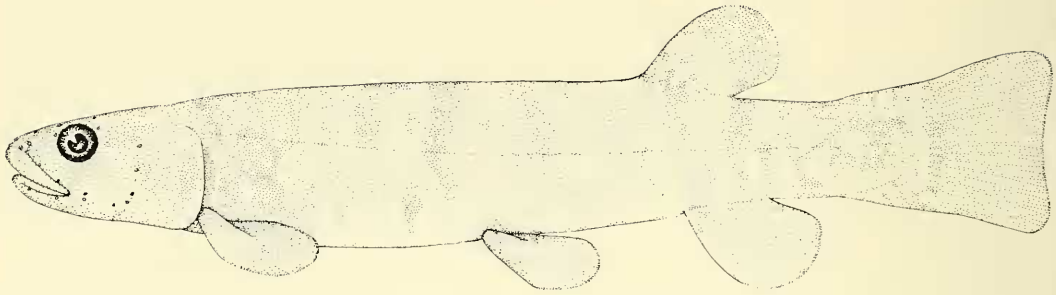
Figure 16. *Galaxias vulgaris* Stokell, 100 mm L.C.F., Maruia River, Buller River System.

most northern lakes of the volcanic plateau to southernmost Fiordland.

Galaxias vulgaris Stokell, 1949
Figure 16

Galaxias vulgaris Stokell, 1949: 491 (holotype: CMCNZ 72, seen; paratype: DMNZ 2069, not seen; locality: Rubicon River, Springfield, Canterbury).

Galaxias anomalus Stokell, 1959b: 265 (holotype: DMNZ 2776, seen; locality: the outlet of a spring which is drained by a ditch crossing the Ophir-Omakau Road a few chains north-east of the Ophir Hotel[1]).

Diagnosis. Differs from *G. brevipinnis* Günther (Fig. 10) in characters noted in the diagnosis of that species (p. 363).

Taxonomy. Stokell (1949: 491, 1959b: 256) has recognized two moderately large and slender species from upland, eastern South Island streams, in addition to *G. brevipinnis.* Populations of fishes of this type are present in most of the major river basins in the east of the South Island, from the Conway River south to the Waiau (Southland), and collection localities are numerous. *G. vulgaris* was recorded by Stokell from Canterbury, the Waiau River (Kaikoura) to the Rakaia, and *G. anomalus* from streams in Central Otago. He did not discuss differences between *G. anomalus* and *G. vulgaris,* but the chief differences between his descriptions of the two species are head length—4.2–4.8 in standard length in *G. vulgaris* and 5.1–5.3 in *G. anomalus*—and in the length of the gill rakers—"long" and "very short" respectively. The two species are indistinguishable from meristic data published by Stokell. Examination of samples from 15 localities indicated that they form a single rather variable species such that the differences between *G. vulgaris* and *G. anomalus,* as defined by Stokell, are absorbed in inter-populational differences. The holotype of *G. anomalus,* though recorded from a drain, is typical of *G. vulgaris* as found in the shingly streams of the upper Clutha River system.

Description. Trunk moderately slender, belly often deepened and rounded, somewhat flattened dorsally with moderate development of a middorsal furrow, trunk profiles somewhat parallel; depressed anteriorly on head, somewhat more slender posteriorly on caudal peduncle, which is moderately long, and somewhat longer than deep. Lateral line a moderately developed midlateral groove, accessory lateral line not observed. Head long and blunt, rounded, much broader than deep. Lower jaw receding a little; jaws long in head, cleft moderately oblique, reaching to about middle of eye; lower jaw profile from ventral aspect moderately broad and shallow. Eye of moderate size, towards upper head profile, interorbital convex to flat.

[1] Omakau is almost directly north of Ophir; the Ophir-Omakau Road at the Ophir Hotel runs in a northwest–southeast direction, so that I could find no locality agreeing with Stokell's description. This area is a part of the Mahinurikia catchment, a Clutha River tributary, and samples were collected in this catchment, not far from Ophir.

Jaws with moderate development of canines laterally; mesopterygoidal teeth strong; pyloric caeca long; gill rakers weak to moderate.

Fins small and fleshy; median fins short-based, but fin extending well toward caudal base, well-rounded distally; anal origin well behind dorsal origin. Pelvic fin inserted somewhat behind midpoint of standard length, fin moderately long in pelvic-anal interval, which is long. Pectoral fin inserted low lateroventrally, fin lamina usually directed ventrally; fin of moderate length and rounded in outline with middle rays longest. Caudal fin moderately long, emarginate, lobes of fin rounded, depth about equal to body depth; caudal peduncle flanges moderately developed.

Coloration. Basic body color brownish to olive, trunk covered dorsally and laterally with irregular and variably dense vermiculations, these disappearing ventrally, sometimes bold blotches, regular chevron-shaped bands, or grading to an almost uniform darkening on the dorsal and dorsolateral trunk.

Size. G. *vulgaris* has been found up to 150 mm long, and seems to commonly reach 100–115 mm.

Variation. Meristic: dorsal 7 (4), 8 (74), 9 (106), 10 (24), 11 (1); caudal 14 (15), 15 (12), 16 (163), 17 (4), 18 (2); anal 8 (7), 9 (54), 10 (96), 11 (29), 12 (4); pelvic 6 (4), 7 (174), 8 (13); pectoral 10 (2), 11 (27), 12 (68), 13 (70), 14 (18), 15 (7), 16 (2); branchiostegals 5 (1), 6 (12), 7 (130), 8 (39), 9 (2); vertebrae 49 (3), 50 (28), 51 (75), 52 (144), 53 (99), 54 (60), 55 (18), 56 (1), 57 (1); gill rakers 2–7 (2), 2–8 (5), 2–9 (3), 2–10 (4), 3–6 (1), 3–7 (9), 3–8 (36), 3–9 (36), 3–10 (10), 4–7 (1), 4–8 (7), 4–9 (8). Morphometric: see Table 2, p. 365.

Population differences. As I define the species, G. *vulgaris* is rather variable, comparable in variability to G. *divergens* and *N. apoda.* These three species are also the most wide-ranging species that are confined to fresh water and which are thus less able to disperse from one river basin to another, by marine routes. Gene flow tends therefore to be limited to population exchanges by means of stream capture and perhaps occasional extraordinary flood situations, when waters of two neighboring catchments become confluent temporarily. In recent years, contact between river systems has been increased by the construction of irrigation canals that transfer water from one catchment to another, but nothing is known of the effect of these changes on the populations of G. *vulgaris.*

The magnitude of variability in G. *vulgaris* can be seen in Figures 17–19, in which various morphological characters are shown with the populations listed in approximately north–south order. It is not easy to arrange the populations in an order likely to express a temperature gradient, since the nature of the watersheds in which these populations occur and their altitude in the headwaters are very variable, even in cases of closely adjacent localities; e.g., the Hinds River drains coastal hills, whereas the nearby Ashburton River penetrates deep into the Southern Alps, which reach well over 7,000 feet in the headwaters of the river. Similarly in the Clutha River System, the Poolburn and Cardrona Rivers are at similar altitudes, but the Poolburn derives its water from the low Rough Ridge, rising to less than 3,500 feet, whereas the Cardrona drains the higher Crown Range, reaching more than 6,000 feet. In comparing populations from the various rivers and trying to relate differences to water temperatures, it is important to realize that even though populations may have occurred at similar altitudes, or be in close proximity to each other, temperatures may be very different, because of the origin of the water. Water temperatures will be a function of altitude, latitude, and the nature of the watershed in the hinterland of the river, and since there is no way to relate these factors and predict water temperatures, it is not pos-
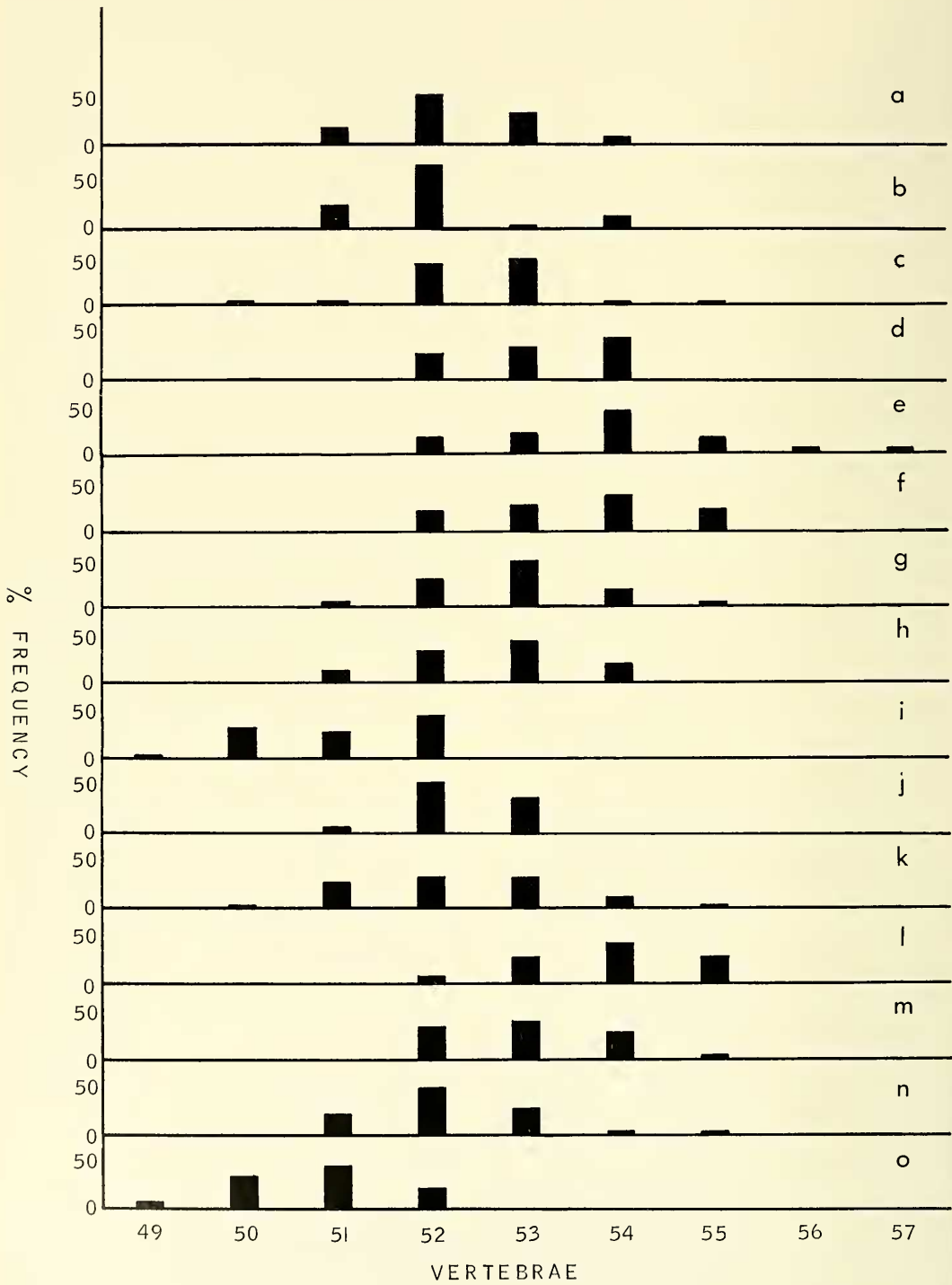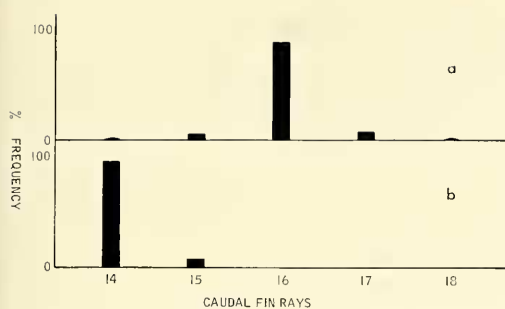
Figure 18. Variation in caudal fin ray number in *Galaxias vulgaris*. a, Other populations of *Galaxias vulgaris* (190 examples); b, Linnburn Stream, Taieri River System (15 examples).

siderably from the bulk of the populations studied.

In some of the more variable morphometric characters, somewhat clinal change is exhibited along a north-south axis, although various and different populations were found to be aberrant and not to relate to the general trends. Head length/standard length (Fig. 19C), length of caudal peduncle/standard length and pre-dorsal/pre-anal length (Fig. 19A) ratios were all found to exhibit this tendency to some extent. These differences cannot justifiably be related to temperature or any other ecological parameter, with our present understanding of the species.

Coloration was found to vary greatly. As in other characters, the Linnburn population was most unusual, being much darker, the trunk patterning almost black. In this species, color pattern seems to be related to habitat. The more northern Canterbury populations occurred in swift, shingly streams in wide, open valleys, with sometimes milky water derived from snow fields. These fishes tended to have olivaceous coloration and a diffuse color pattern. Further to the south, the fishes from Central Otago were much more boldly colored, the vermiculations being similar in form to those in the Canterbury fishes, but contrasting much more with the ground color. These fishes were generally collected from small, stable, clear-flowing streams, and these color differences appear to be related to differences in lighting conditions in the respective habitat types— diffuse, dim but rather constant lighting in the open but somewhat murky alpine Canterbury streams, but broken lighting, interrupted also by marginal stream cover, in the clear flowing Central Otago streams.

sible to relate character differences to water temperatures. Vertebral number, which responds to temperature differences, was found to be very variable, but this variation was irregular; most populations were found to have a range of three to five vertebrae (Fig. 17).

The most distinctive population in the series examined was from the Linnburn Stream, above the Waipori Falls in the Taieri River System. It is distinctive chiefly in the number of caudal fin rays, usually a stable character with 16 rays, but reduced to 14, or occasionally 15 in the Linnburn fishes (Fig. 18). In other meristic characters, this population is "normal." Body depth at vent/standard length and depth of caudal peduncle/length of peduncle ratios for the Linnburn fishes showed that they are stouter than other populations in this species (Fig. 19B). Head length/standard length ratio is also higher than in most, but several other populations, e.g., those in the Hurunui and Cardrona Rivers (Fig. 19C) were also found to differ con-

Figure 17. Variation in vertebral number in *Galaxias vulgaris*, localities in north-south order. a, Conway River (31 examples); b, Waiau River (27 examples); c, Maruia River, Buller River System (26 examples); d, Hurunui River (18 examples); e, Rakaia River (19 examples); f, Ashburton River (29 examples); g, Hinds River (25 examples); h, Waitaki River (28 examples); i, Cardrona River, Clutha River System (35 examples); j, Shag River (33 examples); k, Poolburn River, Clutha River System (41 examples); l, Totara Stream, Taieri River System (15 examples); m, Linnburn Stream, Taieri River System (15 examples); n, Aparima River (28 examples); o, Wilanda Downs Stream, Waiau River System (Southland) (40 examples).
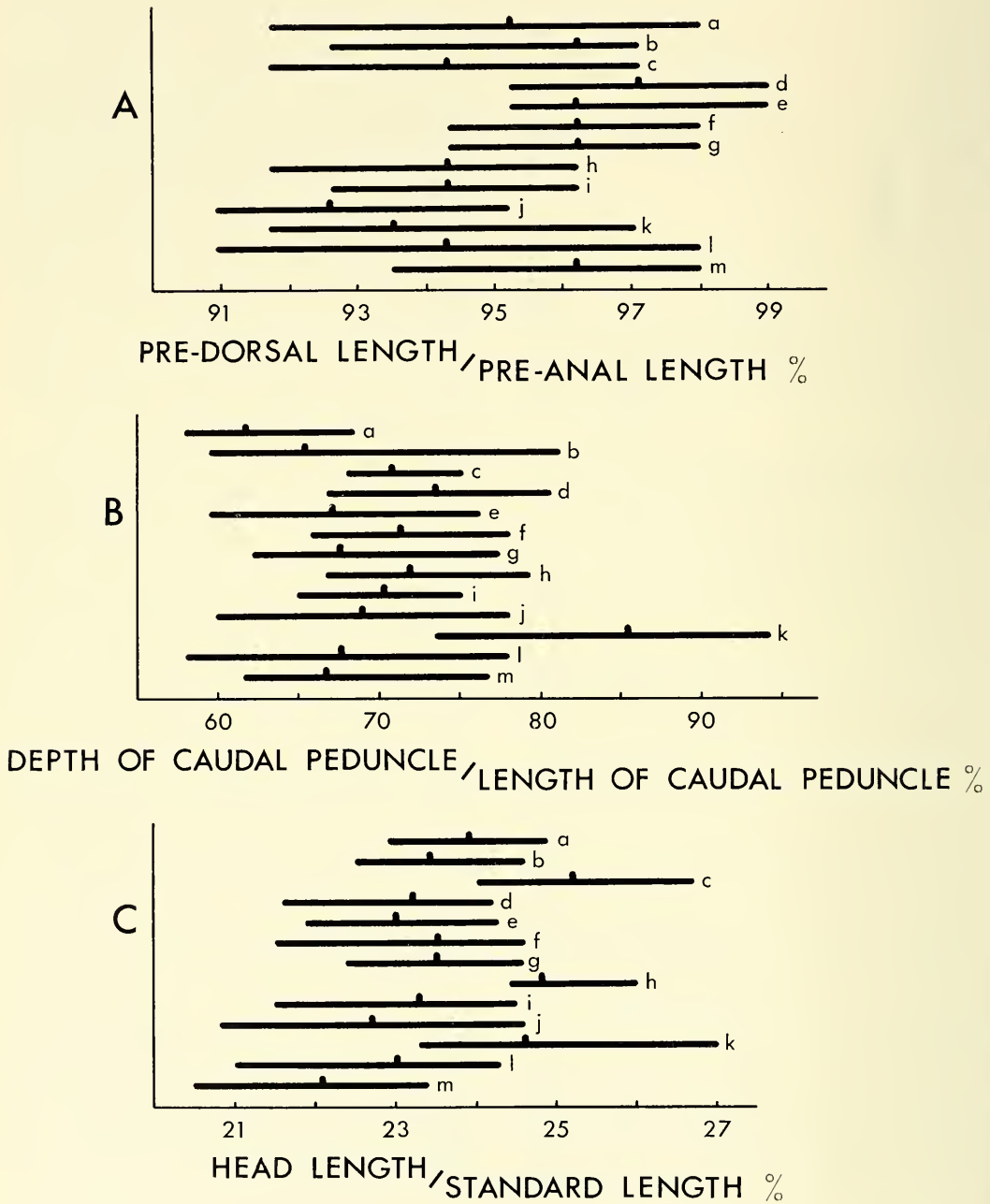
Figure 19. Variation in body proportions in *Galaxias vulgaris*, localities in north-south order. A, Predorsal length/preanal length ratio; B, Depth of caudal peduncle/length of caudal peduncle ratio; C, Head length/standard length ratio; a, Conway River (15 examples); b, Waiau River (15 examples); c, Maruia River, Buller River System (15 examples); d, Hurunui River (15 examples); e, Rakaia River (13 examples); f, Ashburton River (30 examples); g, Hinds River (15 examples); h, Cardrona River, Clutha River System (15 examples); i, Shag River (15 examples); j, Paalburn River, Clutha River System (15 examples); k, Linnburn Stream, Taieri River System (14 examples); l, Aparima River (15 examples); m, Wilanda Downs Stream, Waiau River System (Southland) (15 examples).

This is an interesting species, in which the study of inter-populational variation appears to be potentially profitable and to warrant further investigation. Since the populations occur in widely separated river basins, it is probable that at least some of the variation is simply a product of mosaic evolution. Further examination of the Linnburn population may, however, show that subspecific or specific distinctness has been attained.

Habitat. G. *vulgaris* lives normally in water type similar to that in which *G. brevipinnis, G. prognathus,* and particularly *G. paucispondylus* are found. In Canterbury, most of the cold upland rivers thread their way back and forth over broad, unstable flood plains. *G. vulgaris* occurs commonly in these rivers and their tributaries, mostly in the very fast and broken water. Further south, in Central Otago and Southland, the terrain is more stable, and the upland rivers are usually narrower and more strictly confined to their river courses. In these rivers and their tributaries, *G. vulgaris* also occurs in the rapid and broken water. It has generally not been found in streams entering lakes, although the Hurunui River, above Lake Sumner, is an exception.

G. vulgaris is a typical, highly secretive galaxiid, and is found in the interstices of boulder rapids; it sometimes hides in marginal cover, where this is present. The claim has been made that *G. anomalus* can withstand droughts, like the mudfishes (*Neochanna* species), but I know of nothing to substantiate it, and I think it is doubtful that a species usually found in cold, swiftly flowing streams can aestivate.

Life history. G. *vulgaris* is restricted throughout its life to flowing fresh waters, it has no whitebait juvenile, and probably has no migration of any magnitude. Larvae have often been collected with the adults, suggesting that spawning occurs in or near the customary adult habitat.

Samples collected in December and January invariably contained only spent or rejuvenating fishes; some collected in April and May were showing considerable advance towards gonad maturity, while samples collected in October were mostly freshly spent, although a few individuals were ripe. Recently hatched larvae, 10–15 mm long, were collected in December. These data all suggest that spawning occurs in the early and middle spring, agreeing partly with Stokell's (1955: 25) observation of spawning in winter and early spring. The larvae may be found swimming in small groups in backwaters and slack water at the edges of the streams.

The eggs are moderately large, measuring about 1.5 mm diameter when ripe, and relatively few in number. The largest ripe female examined was 83 mm long and contained 865 eggs.

Distribution. G. *vulgaris* occurs only in the South Island, chiefly on the east of the Southern Alps and the Kaikoura Ranges, but it has extended its range over the alps into the upper Buller River System. It is known from the following localities: Upper Buller River System near Maruia Springs (Fig. 20: 1*); Conway River (2*); Mason, Wandle, and Leeds Rivers, Waiau River System (3*); Hurunui River above Lake Sumner (4*); Cass River (5), Porter River (7), and Rubicon River (8) in the Waimakariri River System (Stokell, 1949: 491); Ashley River and Selwyn River (Stokell, 1949: 491); Wilberforce River (6) and Harper and Avoca Rivers (6a*), Rakaia River System; North Branch (9*) and Taylor's Stream (10*), Ashburton River System; Hinds River (12*); Rangitata River at Mesopotamia (11*); Orari River at Peel Forest (13); Haehaemoana River, Opihi River System (14); tributary of Lake Pukaki (Stokell, 1955: 25); Waitaki River at Otematata (15*); Shag River (17*); Swinburn (18*), Totara (20*), and Linnburn (21*) Streams, Taieri River System; Cardrona (16*) and Poolburn (19*) Streams, Clutha River System; Mataura River (22); Aparima River (23*); Orawia

Figure 20.   Distribution of *Galaxias vulgaris* (numbers in figure as in text, p. 377).

River and Waiau River at Wilanda Downs (24*).

Galaxias maculatus (Jenyns, 1842)
Figure 21

Mesites maculatus Jenyns, 1842: 119 (holotype: BMNH 1917.7.14.6, not seen; paratypes (3):

BMNH 1917.7.14.7–9, not seen; locality: fresh water brook, Hardy Peninsula, Tierra del Fuego).

Mesites attenuatus Jenyns, 1842: 121 (holotype: BMNH 1917.7.14.11, not seen; locality: fresh water, Bay of Islands, New Zealand); Richardson, 1843: 26.

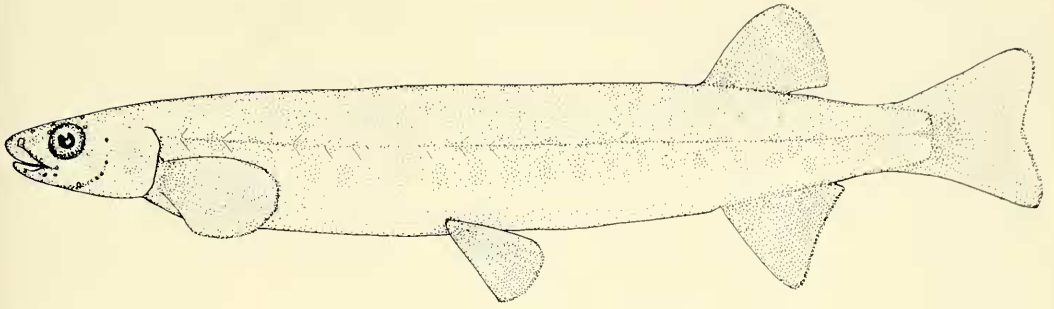*Galaxias attenuatus:* Valenciennes, *In* Cuvier and

Figure 21. *Galaxias maculatus* (Jenyns), 94 mm L.C.F., Ship Creek, South Westland.

Valenciennes, 1846: 348; Günther, 1866: 210;
Hutton, 1872: 60, 1896: 317; Clarke, 1899: 78;
Hutton, 1904: 51; McKenzie, D. H., 1904: 122;
Regan, 1905: 368; Phillipps, 1919: 211, 1924a:
117, 1926b: 292, 1927a: 13; Hope, 1928: 389;
Stokell, 1949: 479; McDowall, 1967b, 1968b.
Galaxias forsteri: Kner, 1865: 320 (not *G. forsteri*
Valenciennes, *In* Cuvier and Valenciennes,
1846: 351).
Austrocobitis attenuatus: Ogilby, 1899: 158.
Galaxias maculatus attenuatus: Stokell, 1966: 78.

Diagnosis. Differs from *G. usitatus* Mc-
Dowall (Fig. 23) in having more vertebrae
and pelvic fin rays, shorter head with
smaller eye, longer pelvic-anal interval,
and the presence of a marine whitebait
stage. Differs from *G. gracilis* McDowall
(Fig. 24) in having a much higher vertebral
count, more dorsal fin rays, more branchios-
tegals and many fewer gill rakers; also in
more anterior pelvic fin insertion, shorter
pelvic-anal interval, much shorter head,
broader interorbital, and smaller eye.

Description. Slender bodied, trunk
rounded, somewhat compressed and deeper
than broad, much more slender on head
and on caudal peduncle, which is short and
very slender, depth much less than length.
Lateral line a well-developed mid-lateral
furrow; accessory lateral line not evident.
Head small and slender, short; eye large,
moderately deep in head, interorbital con-
vex and moderately broad in head width,
but head itself narrow; jaws short, about
equal in length, cleft reaching to about
anterior eye margin, slightly oblique, gape
very narrow; profile of lower jaw from

ventral aspect deep and rather narrow, U-
shaped. Canine teeth lacking from jaws;
mesopterygoidal teeth well developed; gill
rakers well developed; pyloric caeca rudi-
mentary or absent.

Median fins rather small, membranous.
Dorsal fin origin well back, fin short based,
greatest length not much greater than basal
length, distal margin of fin somewhat
rounded. Anal origin more or less below
dorsal origin, greatest fin length very little
greater than basal length, distal margin of
fin straight or concave, inclined to trunk
axis, anterior rays much the longest. Pec-
toral fin short in rather long pectoral-pelvic
interval, fin inserted high laterally. Pelvic
fins very short in long pelvic-anal interval,
insertion somewhat behind midpoint of
standard length. Caudal fin short, forked,
depth sub-equal to body depth; caudal
peduncle flanges weakly developed.

Variation. Meristic: dorsal 9 (7), 10
(58), 11 (59), 12 (4), 13 (2); caudal 15
(1), 16 (80); anal 14 (7), 15 (31), 16
(53), 17 (36), 18 (5); pelvic 6 (1), 7 (80);
pectoral 11 (4), 12 (28), 13 (62), 14 (17),
15 (3); branchiostegals 5 (9), 6 (93), 7
(73), 8 (5); vertebrae 59 (1), 60 (13), 61
(44), 62 (45), 63 (24), 64 (5); gill rakers
3–10 (2), 3–11 (3), 4–10 (10), 4–11 (15),
4–12 (3), 5–10 (4), 5–11 (1), 5–12 (1).
Morphometric: see Table 3, p. 380.

Coloration. Trunk pale creamish white,
covered with greenish gray mottling dor-
sally and laterally, mottling failing latero-
ventrally and ventrally and varying from

TABLE 3. MORPHOMETRIC VARIATION IN SHOALING SPECIES (FIGURES GIVEN AS PERCENTAGES OF DE-NOMINATOR OF RATIO).

	G. maculatus			G. usitatus			G. gracilis		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	87.7	90.9	91.7	88.5	89.3	90.1	87.7	89.3	91.7
B.D.V./S.L.	10.3	11.6	12.9	9.9	11.5	13.0	10.5	11.2	12.1
L.C.P./S.L.	8.8	10.5	12.3	8.6	9.9	10.9	10.4	11.8	13.4
D.C.P./L.C.P.	49.0	59.5	68.5	59.2	66.7	76.3	48.1	54.4	64.9
Pre D./S.L.	74.6	76.9	78.7	74.1	76.3	78.7	73.0	74.6	78.1
Pre D./Pre A.	96.2	99.0	102.0	96.2	98.0	101.0	97.1	100.0	103.1
D.F.B./S.L.	7.8	9.1	11.3	8.5	10.1	12.5	7.2	7.9	9.2
D.F.B./D.F.M.	58.5	70.4	82.0	61.0	68.5	77.5	58.5	65.8	72.5
A.F.B./S.L.	11.8	13.7	15.6	12.2	13.6	15.1	13.0	14.2	15.5
A.F.B./A.F.M.	78.1	84.0	90.9	75.2	81.3	87.0	75.2	84.8	90.1
Pre Pel./S.L.	48.8	50.9	52.9	49.5	52.9	55.6	53.1	54.6	56.2
Pec.Pel./S.L.	29.9	32.2	34.7	27.5	30.3	33.1	28.4	31.4	35.1
Pec./Pec.Pel.	30.7	35.3	42.2	35.6	39.0	43.2	32.3	36.9	42.4
Pel.An./S.L.	24.4	27.7	30.2	21.9	25.4	27.2	20.0	21.6	24.0
Pel./Pel.An.	29.4	36.8	44.0	37.1	43.4	49.1	40.9	45.6	50.0
H.L./S.L.	18.5	20.0	21.6	22.0	23.5	24.6	22.8	24.3	25.5
H.D./H.L.	43.7	48.8	52.9	42.9	46.3	50.0	42.9	48.1	52.4
H.W./H.L.	45.1	51.6	56.2	43.7	48.8	53.5	46.7	49.3	53.5
Sn.L./H.L.	26.5	28.5	33.3	25.9	28.7	32.6	25.9	27.9	31.3
P.O.H.L./H.L.	48.5	53.2	58.5	49.0	50.3	53.8	50.0	54.4	59.2
Io.W./H.L.	34.3	37.6	41.3	30.8	33.9	37.5	28.6	31.0	33.2
D.E./H.L.	19.5	21.8	23.7	21.8	24.3	26.9	22.2	24.3	27.3
L.U.J./H.L.	28.4	31.1	35.7	31.7	34.4	37.0	28.0	30.8	34.1
L.M./H.L.	25.6	28.7	32.5	28.6	32.9	36.9	26.1	28.5	33.3
W.G./H.L.	25.0	29.0	32.9	26.3	28.9	34.5	25.0	27.1	30.4
Fish examined		40			20			30	

fine speckling to bold, irregular blotches. The belly, opercular covers, and eyes are silvery. The head is usually darker than the rest of the trunk, the fins almost colorless, except for a few melanophores along the fin rays and at the base of the caudal fin.

Size. G. maculatus is known to grow to 169 mm, and commonly reaches 100–110 mm.

Population differences. Examination of 80 fishes from the Waikanae River and 51 from the Awarua River, localities about 400 miles apart, revealed no meristic differences between these populations. Samples from more distant Australian and South American populations have shown that there are clinal differences in some characters (McDowall, 1967b).

Habitat. G. maculatus is found in diverse habitat types, but appears to be most successful in small, stable, coastal and lowland streams, chiefly in gently flowing water, usually above tidal influence. Large shoals are often found in back-waters and similar areas where the water is slack. It is abundant in the darkly tannin-stained waters of bush and flax swamps and streams on the west coast of the South Island. However, *G. maculatus* inhabits a wide variety of water types, including quite swift, gravelly streams, where the shoals appear to break up, and the fish are usually found singly, or in twos and threes in cover at the stream margins. Upstream range of *G. maculatus* is usually very limited. Compared with other galaxiids, it has very poor climbing ability, and it is limited to streams below falls that other whitebait species are able to surmount. *G. maculatus* is probably the most prolific, open-living, and commonly encountered species of *Galaxias*.
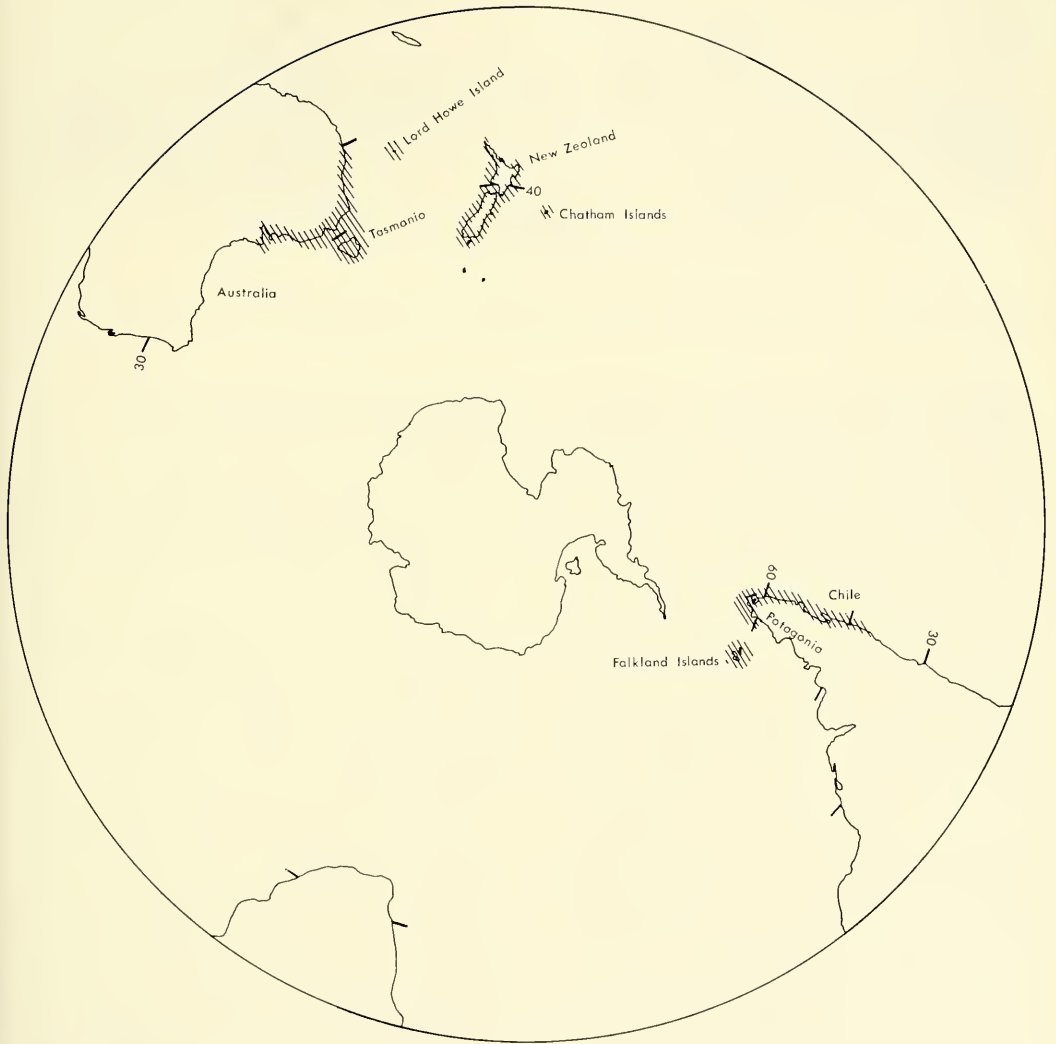
Figure 22.   Distribution of *Galaxias maculatus*.

Life history. Because of its economic importance in the New Zealand whitebait fishery, the life history of *G. maculatus* has been extensively studied (Hayes, in Hefford, 1931a, b, 1932; McKenzie, M. K., n. d.; Benzie, 1961; Burnet, 1965; McDowall, 1968b).

G. maculatus is peculiar in that it breeds amongst grasses on estuarine flats and that breeding occurs in synchrony with the high spring tides. The ripe fish migrate downstream into estuaries in large shoals and swim out over tidal flats covered by the exceptional tides at the full and new moons. The eggs are deposited amongst the bases of terrestrial plants, mostly grasses and sedges, and are left exposed when the tide recedes. They hatch at subsequent spring tide cycles and the larvae are washed out into the sea. The

Figure 23.   *Galaxias usitatus* McDowall, 72 mm L.C.F., Lake Waiparera, North Auckland.

eggs will tolerate and hatch in water of salinities varying between pure fresh and pure sea water. Spawning is reported from September t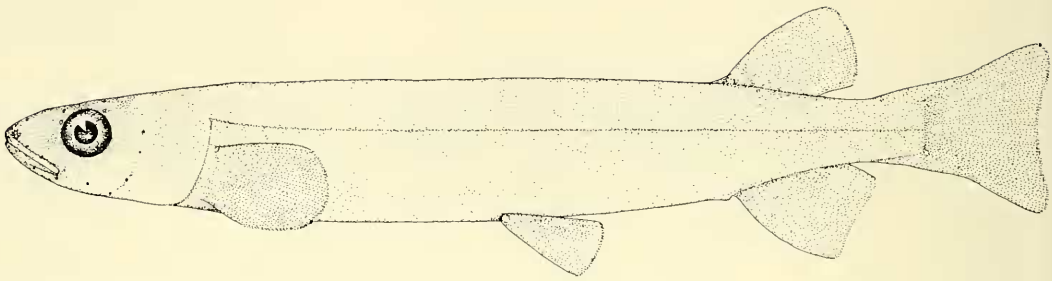o June, but occurs mostly in the autumn, from March to May. The transparent whitebait juveniles (Fig. 40) migrate into fresh water during all months of the year, but most commonly in the spring, from August to November. Size at migration is mostly between 45 and 55 mm. The marine life lasts over the winter period between the autumn spawning and the subsequent spring migration. Most adults reach maturity at one year and are thought usually to breed only once. In exceptional cases, maturation is delayed for a further one or even two years, and some fish may survive an initial spawning and perhaps spawn again.

The eggs are small, measuring about 1 mm diameter when ripe, but size is variable. Fecundity was found to vary from 137 to 13,000 in fishes between 47 and 135 mm long (McDowall, 1968b). Compared with other galaxiids examined, egg number is high.

Distribution. *G. maculatus* is known from all over New Zealand, in coastal situations, and also on the Chatham Islands. It occurs in southeastern Australia, Tasmania, Lord Howe Island, Southern Chile, Patagonia, and the Falkland Islands. With *Geotria australis,* the southern lamprey, which has a similar range, it is probably the most widely dispersed species of freshwater fish known (Fig. 22).

Galaxias usitatus McDowall, 1967
Figure 23

Galaxias usitatus McDowall, 1967a: 7 (holotype: NZMD, seen; paratypes: DMNZ 4,500, seen; MCZ 45054, seen; USNM 201223, seen; locality: Lake Waiparera, near Kaitaia, North Auckland).

Diagnosis. Differs from *G. maculatus* (Jenyns) (Fig. 21) in characters noted in the diagnosis of that species (p. 379); differs from *G. gracilis* McDowall (Fig. 24) in having more vertebrae, more branchiostegals, fewer gill rakers, a shorter pelvic-anal interval, longer dorsal fin base, shorter caudal peduncle, the presence of serrations on the free margin of the operculum and the greater size attained.

Description. Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle, which is slender and short. Lateral line an indistinct midlateral furrow; accessory lateral line not evident. Head long and slender, about as broad as deep. Eye large, close to upper head profile, interorbital more or less flat, broad relative to head width. Jaws equal and prominent, cleft slightly oblique, reaching to about anterior eye margin, gape rather narrow; profile of lower jaw from ventral aspect a deep and rather narrow U. Jaws without canines; mesopterygoidal teeth well developed; pyloric caeca lacking; gill rakers well developed; free margin of opercular membrane finely serrate.

Fins membranous and short, except anal, which is long based. Dorsal fin origin well
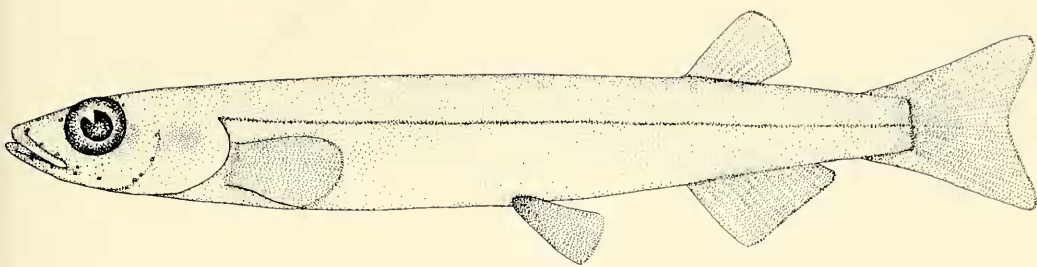
Figure 24.   *Galaxias gracilis* McDowall, 59 mm L.C.F., Upper Lake Rotatuna, North Auckland.

back, fin with moderately short base, maximum fin length somewhat longer than fin base, distal margin of fin slightly rounded. Anal fin origin more or less below dorsal origin; fin long based, but greatest fin length little greater than basal length, distal margin of fin about straight, inclined to trunk axis. Pelvic fin inserted at about midpoint of standard length, pelvic-anal interval short, pelvic fin moderate in pelvic-anal interval, short. Pectoral fin short, inserted rather high laterally. Caudal fin very short, forked, fin depth about equal to body depth; peduncle flanges poorly developed.

Variation. Meristic: dorsal 9 (2), 10 (22), 11 (15), 12 (2); caudal 14 (1), 15 (4), 16 (34), 17 (1), 18 (1); anal 12 (3), 13 (8), 14 (6), 15 (3), 16 (1); pelvic 6 (30), 7 (11); pectoral 11 (1), 12 (5), 13 (21), 14 (12), 15 (2); branchiostegals 5 (1), 6 (25), 7 (15); vertebrae 54 (2), 55 (5), 56 (10), 57 (12), 58 (9), 59 (3); gill rakers 4–11 (2), 4–12 (6), 4–13 (1), 5–11 (5), 5–12 (6). Morphometric: see Table 3, p. 380.

Coloration. Trunk a dusky gray-brown and covered with irregular dark blotches, very similar to *G. maculatus.* In fresh specimens, the lateroventral and ventral abdomen are silvery, but in preserved material, colorless.

Size. G. usitatus is known to grow to 81.5 mm. Examples from a sample collected from the type locality were commonly 60–70 mm long.

Population differences. Only one population of *G. usitatus* is presently known.

Habitat. G. usitatus was collected along the shores of Lake Waiparera, mostly amongst moderately open sedges growing in a few inches to a foot of water. It was also collected in a small, boggy, overgrown tributary that drains partly cleared manuka (*Leptospermum* sp.) scrublands. It is mostly a midwater swimming and shoaling species.

Life history. Nothing is known of the breeding of *G. usitatus,* except that it must occur either in the lake or in the small tributary stream running into the lake. Population size in the tributary stream in March, when specimens were collected, was extremely low, so that if spawning does occur there, a definite spawning migration of some type must take place. Examination of the gonads showed that in March, the fish are approaching maturity, although breeding appeared to be some time away. The gonads were too immature for useful measurements of eggs or determination of egg number. The eggs appeared to be quite numerous, comparable in number with those of *G. maculatus* of similar size. From the stage of maturity, breeding appears likely to occur in late autumn or early winter.

Distribution. G. usitatus is presently known only from Lake Waiparera, the type locality, and a small stream entering the lake from the south (Fig. 25).

Galaxias gracilis McDowall, 1967
Figure 24

Galaxias gracilis McDowall, 1967a: 6 (holotype: NZMD, seen; paratypes: DMNZ 4499, seen; MCZ 45053, seen; USNM 201224, seen; locality: Upper Lake Rototuna, Kaipara Harbour, North Auckland).

Diagnosis. Differs from *G. maculatus* (Jenyns) (Fig. 21) and *G. usitatus* McDowall (Fig. 23) in characters discussed in the diagnoses of these species (pp. 379 and 382 respectively).

Description. Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle, somewhat deeper than broad. Caudal peduncle short and slender. Lateral line an indistinct lateral furrow; accessory lateral line not evident. Eye large; at upper head profile, interorbital flat, very narrow. Lower jaw protruding a little or equal in length to upper; lips thin, cleft of mouth slightly oblique, extending to about anterior eye margin; gape very narrow, lower jaw from ventral aspect deep and narrow, U-shaped. Jaws without canines; mesopterygoidal teeth moderately developed; gill rakers long; pyloric caeca lacking.

Fins membranous and short, except anal, which is rather long based; anal origin more or less below dorsal origin. Distal margin of dorsal fin rounded to straight, anterior rays longest; margin of anal straight, anterior rays longest, maximum fin length little greater than basal length. Pelvic fins inserted rather posteriorly, pelvic-anal interval short, fin relatively short in pelvic-anal interval. Pectoral fin short, inserted high laterally. Caudal fin short, forked, depth about equal to body depth; caudal peduncle flanges poorly developed.

Variation. Meristic: dorsal 7 (2), 8 (23), 9 (22), 10 (3); caudal 15 (4), 16 (42), 17 (4); anal 12 (2), 13 (7), 14 (29), 15 (13), 16 (1); pelvic 6 (7), 7 (40), 8 (3); pectoral 12 (8), 13 (28), 14 (14); branchiostegals 4 (2), 5 (27), 6 (21), 7 (2); vertebrae 47 (1), 48 (16), 49 (24),

50 (9); gill rakers 5–13 (2), 5–14 (2), 5–15 (1), 6–13 (1), 6–14 (12), 6–15 (7), 6–16 (3), 6–17 (1), 7–16 (1). Morphometric: see Table 3, p. 380.

Coloration. Trunk densely covered with large melanophores that intensify on the head and dorsum of the trunk, failing lateroventrally and ventrally. Fresh specimens are silvery in these latter areas.

Size. *G. gracilis* is known to grow only to 62.5 mm. Many examples in the very large sample collected were between 45 and 55 mm long, but few were larger.

Population differences. Only one population of *G. gracilis* is known.

Habitat. *G. gracilis* has been collected only from a small, coastal dune lake. Large numbers were collected from shallow water near the lake shore.

Life history. The entire life history of *G. gracilis* occurs in fresh water, since the locality from where it is known is landlocked. Ripe males were present in the sample, collected in March, but no ripe or mature females. Breeding thus appears likely to occur some time in the autumn. In a female 47 mm long and approaching maturity, there were 604 eggs, 0.6–0.8 mm in diameter.

Distribution. *G. gracilis* is presently known only from the type locality, Upper Lake Rototuna (Fig. 25).

Galaxias divergens Stokell, 1959
Figure 26

Galaxias divergens Stokell, 1959b: 266 (holotype: DMNZ 2777, seen; locality: a rapid shingly stream flowing into the Marnia River about a mile west of the hot springs).

Diagnosis. Very similar in form to *G. paucispondylus* Stokell (Fig. 29) but differs in its stouter build, slightly shorter caudal peduncle, and more posterior pelvic fin insertion. The chief differences are the very reduced gill rakers and the lower number of fin rays in the pelvic and caudal fins. Differs from *G. prognathus* Stokell (Fig. 31) in its stouter build, the jaws being sub-equal with the upper jaw longer
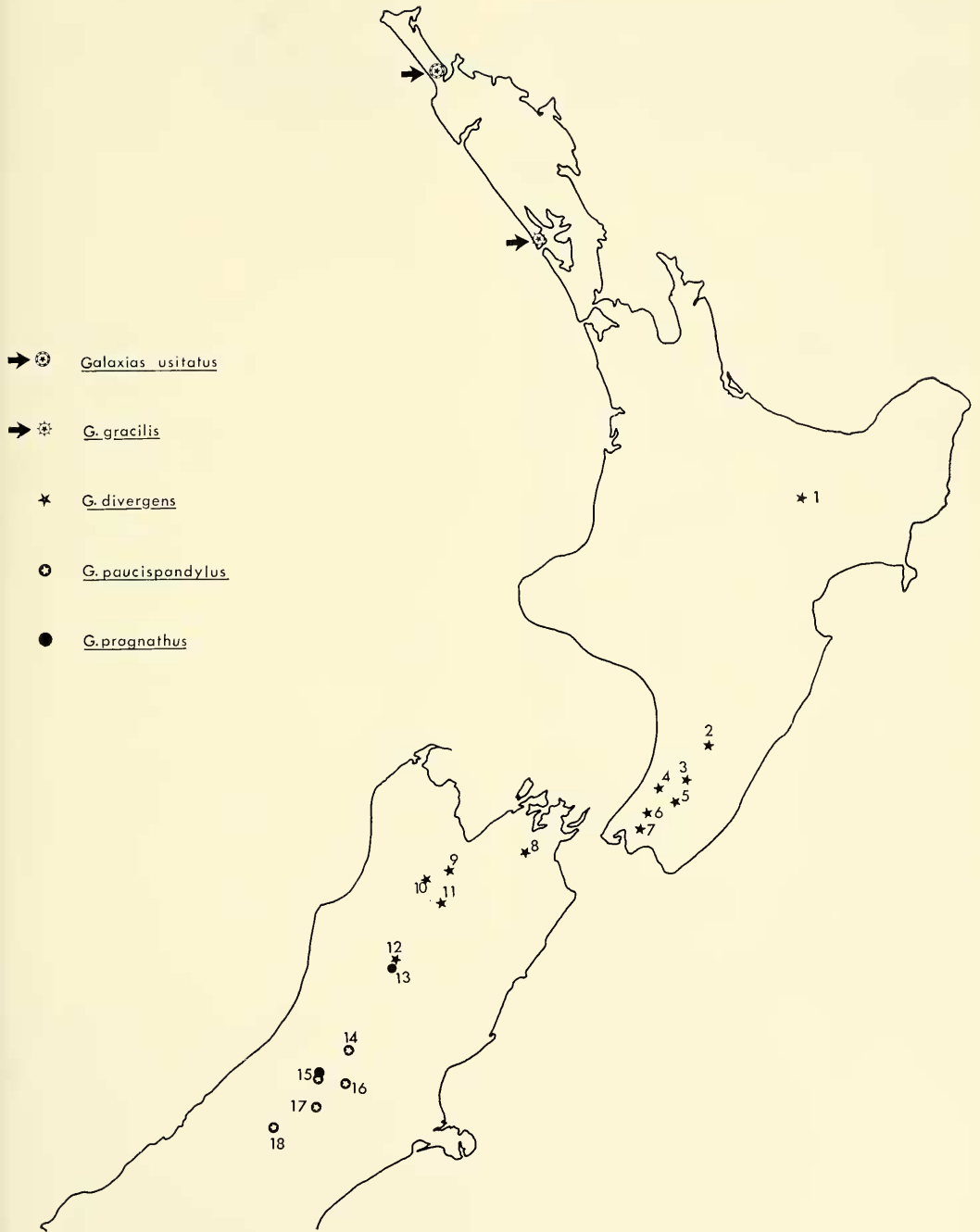
Figure 25. Distribution of *Galaxias usitatus, G. gracilis, G. divergens, G. paucispondylus,* and *G. prognathus* (numbers in figure as in text an pp. 390, 393, and 394).
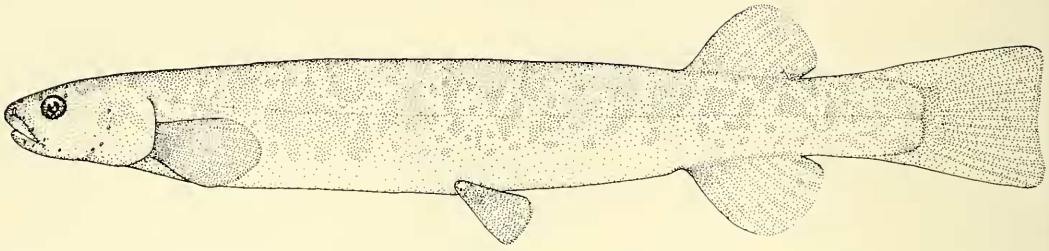
Figure 26.   *Galaxias divergens* Stokell, 68 mm L.C.F., Mountain Camp Stream, Pelorus River System.

in head length, and usually fewer caudal and pelvic fin rays. The difference in jaw form immediately separates the two species.

Description. Trunk rounded to squarish in section, dorsally flattened with moderate development of a middorsal furrow, trunk profiles somewhat parallel, tapering anteriorly to a small head and becoming slender posteriorly. Caudal peduncle very long and generally slender, depth about half length. Lateral line an inconspicuous midlateral groove; accessory lateral line not observed. Head short, broader than deep, head depth conspicuously less than body depth. Eye small, towards upper head profile, and interorbital flat. Jaws equal or lower a little shorter, short in head length; cleft moderately oblique and reaching to about anterior eye margin; jaw profile from ventral aspect broad and shallow, somewhat flattened anteriorly. Jaws without canines, mesopterygoidal teeth weak; pyloric caeca lacking; gill rakers reduced to indefinite stubs.

Dorsal and anal fins small, somewhat fleshy at bases but membranous distally; short based and extending little beyond bases, distal margins rounded. Dorsal origin well forwards due to length of caudal peduncle, anal origin below or a little behind dorsal origin. Pelvic fin inserted at about midpoint of standard length; pelvic-anal interval moderately long, fin very short in interval. Pectoral fin inserted moderately high laterally; short in pectoral-pelvic interval, which is also rather short; distal margin of pectoral fin rounded, with middle rays longest. Caudal fin moderately

long, emarginate, depth about equal to body depth; flanges of peduncle weak to moderate.

Variation. Meristic: dorsal 7 (9), 8 (58), 9 (34), 10 (10); caudal 13 (1), 14 (3), 15 (83), 16 (6); anal 8 (13), 9 (68), 10 (36), 11 (8); pelvic 6 (119), 7 (5); pectoral 9 (17), 10 (59), 11 (41), 12 (7); branchiostegals 6 (11), 7 (64), 8 (44), 9 (4); vertebrae 47 (2), 48 (14), 49 (38), 50 (69), 51 (81), 52 (44), 53 (2); gill rakers—these are so reduced and irregular in development that a satisfactory count was impossible. Morphometric: see Table 4, p. 387.

Coloration. Basic body color usually a striking creamy-white, covered dorsally and laterally with irregular, darker, greenish brown to gray vermiculations, which fail lateroventrally and ventrally. Head usually dark, pigmentation extending down on to cheeks. Less commonly the coloration consists of more diffuse, dark speckling.

Size. G. *divergens* is a small species, which is known to reach only 87 mm. Examples from the type locality were commonly over 70 mm, but those from other localities were generally smaller, usually 60–70 mm long.

Population differences. G. *divergens* has a moderately broad range in the North Island and the northwest of the South Island, and considerable differences between populations were observed. Stokell (1959b: 266) described G. *divergens* from a locality near Maruia Springs, noting that a form "from shingly streams in the Wellington Province agrees with G. *divergens*

Table 4. Morphometric variation in slender, alpine species (figures given as percentages of denominator of ratio).

	G. divergens			G. paucispondylus			G. prognathus		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	85.5	87.7	90.9	84.8	86.2	88.5	86.2	88.5	90.1
B.D.V./S.L.	9.3	11.2	14.1	10.0	11.1	13.6	8.3	9.5	11.9
L.C.P./S.L.	14.7	17.0	18.9	16.8	19.0	21.4	15.3	16.7	18.0
D.C.P./L.C.P.	40.5	52.6	66.7	41.3	45.7	51.8	35.7	42.6	48.8
Pre D./S.L.	67.1	69.9	74.6	65.8	69.0	72.5	67.1	70.9	73.5
Pre D./Pre A.	94.3	98.0	102.0	94.3	97.1	101.0	93.5	95.2	98.0
D.F.B./S.L.	7.2	9.3	12.4	7.6	9.1	11.1	7.2	8.5	9.7
D.F.B./D.F.M.	51.8	61.7	76.9	54.4	62.5	80.0	57.5	64.9	75.7
A.F.B./S.L.	9.1	10.4	13.5	8.4	10.1	11.9	8.6	9.9	11.3
A.F.B./A.F.M.	59.5	68.5	78.7	55.6	64.5	72.5	61.0	70.4	78.7
Pre Pel./S.L.	47.6	50.5	52.9	43.9	47.4	50.5	48.1	50.8	53.2
Pec.Pel./S.L.	29.2	32.3	37.2	26.7	29.4	31.6	30.4	33.4	35.0
Pec./Pec.Pel.	29.6	39.6	48.4	37.9	46.6	54.4	28.6	35.7	42.1
Pel.An./S.L.	19.3	22.4	25.8	19.8	23.5	26.3	20.5	22.9	24.6
Pel./Pel.An.	34.4	45.1	54.2	37.5	45.6	55.6	33.8	39.2	43.8
H.L./S.L.	16.9	19.7	21.9	17.7	19.1	20.8	17.2	18.5	19.8
H.D./H.L.	41.0	49.3	54.6	39.2	48.1	59.5	40.0	44.8	52.6
H.W./H.L.	50.0	59.5	70.9	57.1	61.7	63.3	50.5	54.6	63.3
Sn.L./H.L.	25.6	29.3	33.3	26.5	29.4	34.6	25.0	28.7	31.7
P.O.H.L./H.L.	50.0	54.6	65.4	51.0	56.8	61.4	48.8	51.0	54.4
Io.W./H.L.	32.0	36.9	45.9	27.8	33.4	40.5	31.2	33.4	40.0
D.E./H.L.	16.0	18.2	21.3	12.2	15.0	18.7	12.8	14.1	16.7
L.U.J./H.L.	28.6	35.3	40.0	30.8	34.6	38.8	26.5	29.5	33.3
L.M./H.L.	26.2	31.2	36.0	28.1	30.2	35.1	30.6	32.9	35.6
W.G./H.L.	30.4	35.8	49.3	30.6	35.1	40.3	33.3	35.0	37.7
Fish examined		105			40			23	

in the number of ventral rays and the absence of pyloric caeca but has a head in length ratio of less than five, and a definitely curved mouth." He expressed the view that "the characters concerned are rather more important than come within the author's conception of subspecific distinction."

Populations of fishes like these are now known to be quite widespread. They do not seem to fall into more than one taxon and certainly form an assemblage that stands apart from the other species of the upland-alpine, slender-species group. The differences between the populations are decidedly less than differences between these *G. divergens*-type populations and other species in the species group. Accordingly, all these populations are included in a somewhat variable species, *G. divergens* Stokell.

Meristic characters were found to be similar in all populations and all characters examined. Maxima and minima in dorsal, anal, caudal, and pelvic fin ray counts in no case differed by more than one element between populations, and pectoral ray, branchiostegal, and vertebral counts by no more than two elements. Overlap between populations was thus found to be broad. Vertebral number and pectoral ray number showed slight general increase along a north-south axis (Fig. 27), although in both characters, one population or another was found to interrupt the continuity of the variation. The body proportions were found to exhibit greater variation. Fishes from the Mangatarere population were considerably stouter in build than other populations, this being evident in both the depth caudal peduncle/length of peduncle and body depth at vent/standard length ratios
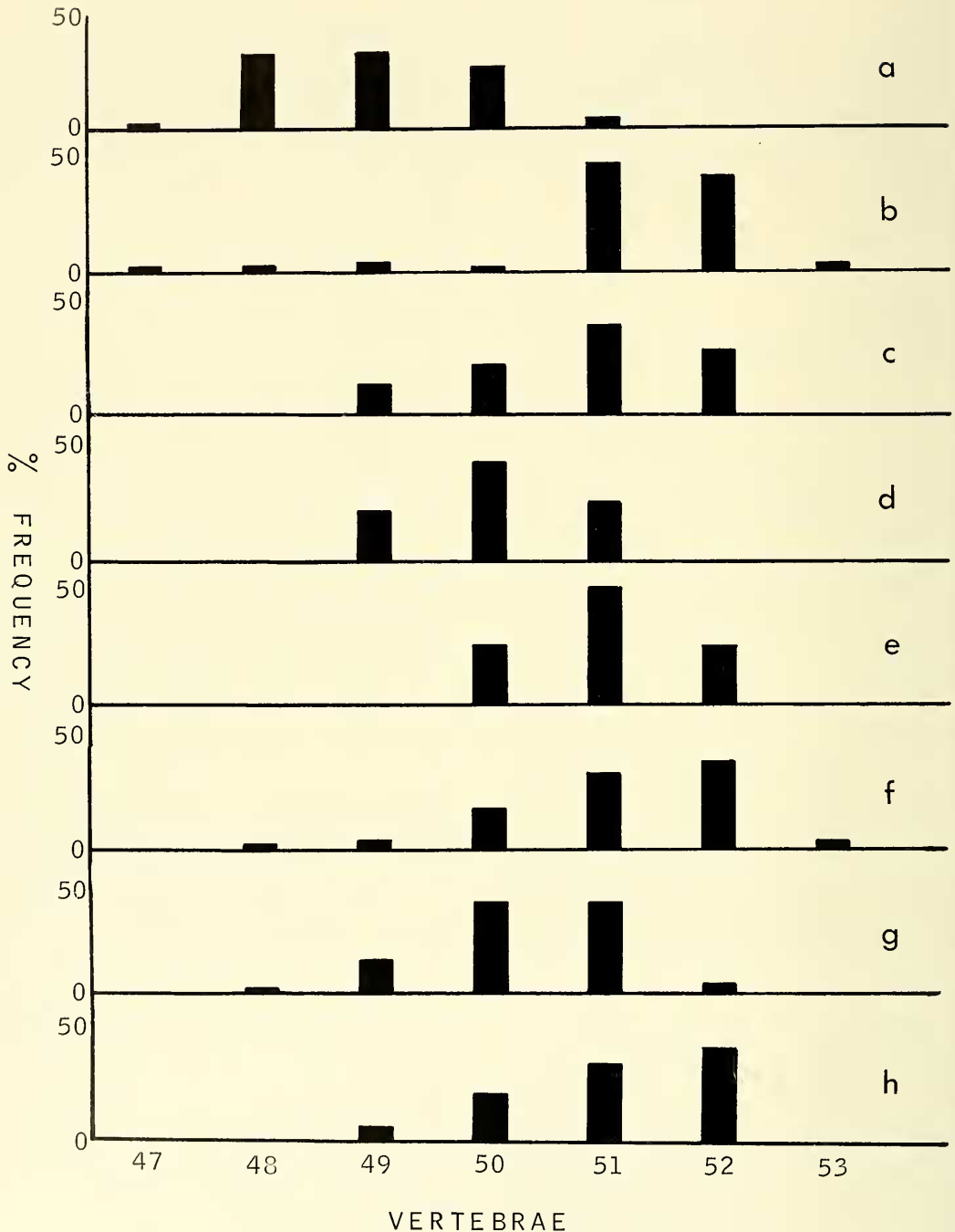
Figure 27. Variation in vertebral number in *Galaxias divergens*, localities in north-south order. a, Tukuhou Stream at Haramanga, Rangitaiki River System (54 examples); b, Hinaki Stream, Ruamahanga River System (74 examples); c, Mangaka-tukutuku Stream, Waikanae River System (54 examples); d, Hutt River (57 examples); e, Catchpool Stream, Wainuiamata River System (23 examples); f, Mountain Camp Stream, Pelorus River System (54 examples); g, Stream at Golden Dawns, Motueka River System (68 examples); h, Maruia River, Buller River System (21 examples).
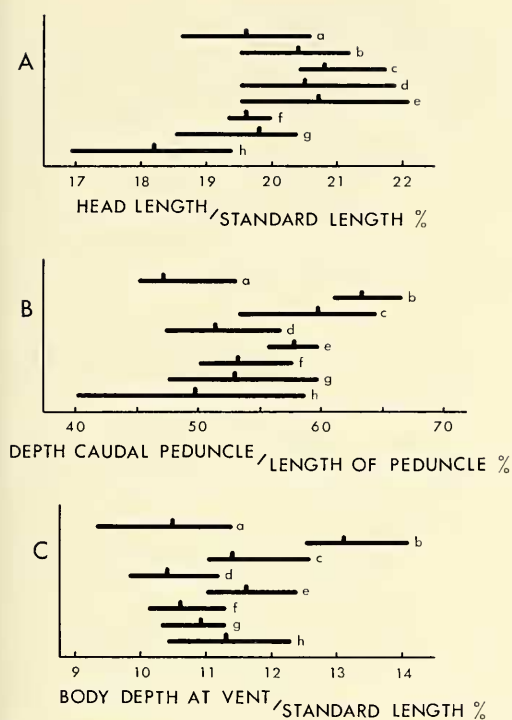
Figure 28. Variation in body proportions in *Galaxias divergens*, localities in north-south order. A, Head length/standard length ratio; B, Depth of caudal peduncle/length of caudal peduncle ratio; C, Body depth at vent/standard length ratio; a, Tukuhau Stream at Haramanga, Rangitaiki River System (20 examples); b, Hinaki Stream, Ruamahanga River System (13 examples); c, Mangakotukutuku Stream, Waikanae River System (9 examples); d, Hutt River (14 examples); e, Catchpool Stream, Wainuiamata River System (10 examples); f, Mountain Camp Stream, Pelorus River System (10 examples); g, Golden Dawns Stream, Matueka River System (10 examples); h, Maruia River, Buller River System (17 examples).

(Fig. 28B, C). The Catchpool and Mangakotukutuku populations were also somewhat more stout than the others. Head length is less variable, except that the sample from the type locality, at Maruia, stands distinctly apart from all other populations (Fig. 28A). There is no obvious basis for this variability, and despite its extent, there appears to be only one taxon here, at the species level. Until the range of this species is thoroughly understood, it is not appropriate to name sub-species.

It seems likely that many more localities for *G. divergens* within the known range, and particularly between those in the southern Wairarapa and the disjunct population at Horomanga, will be discovered. Data from these may make the inter-population variation more comprehensible.

Habitat. G. divergens is usually captured from small, moderately swiftly flowing headwater streams, which have gravel or boulder beds. Streams where *G. divergens* is abundant are usually stable, and often occur in narrow, steep gullies with little or no flood plain. The characteristic water type is turbulent but not broken; the fish characteristically live in the interstices of the stream substrate, and are almost always hidden.

Life history. G. divergens is restricted to fresh water and has been found only in flowing water, although a population is known in a tributary of Lake Rotoiti. Fishes collected from the Maruia, Golden Downs, Mountain Camp, and Catchpool populations in May were near maturity; others, taken in the Mangakotukutuku in September, the Catchpool and Hutt localities in November, and the Horomanga in December appeared to be mature. Adults in a large sample from the Mangatarere, collected in late February, were found to be spent, and the sample contained many small juveniles, mostly between 20 and 25 mm long. Recently hatched juveniles 10–12 mm long were collected from the Hutt River at Kaitoke in early February. These data suggest a rather extended spawning period in the spring and summer.

The eggs of *G. divergens* are of moderate size, 1.3–1.6 mm diameter, and very few in number, a female of 68 mm carrying 225 eggs. The breeding site is unknown to me. A search was made for the site when fishes were collected during December, when there were ripe fish in the population, and it was not discovered (G. A. Eldon, pers. comm.). Mature fish from the Horomanga locality exhibited a peculiar sex ratio, all the fish being females. The failure to find
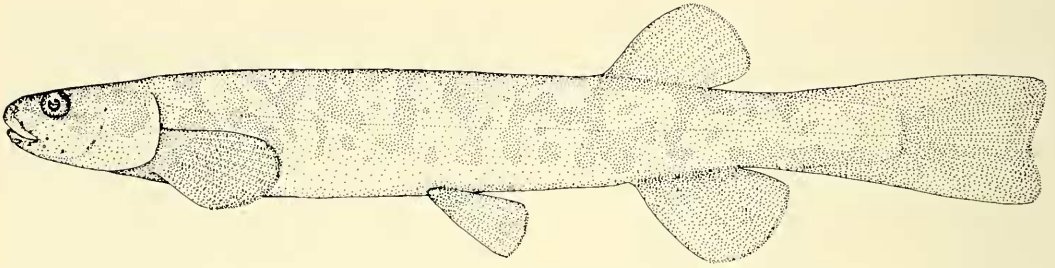
Figure 29. *Galaxias paucispondylus* Stokell, 70 mm L.C.F., Wilberforce River, Rakaia River System.

the spawning site may be related to a spawning migration in association with breeding, perhaps explaining the absence of males from the Horomanga sample.

Groups of juveniles may be found swimming freely in the still waters amongst rock piles at the edges of the pools and other places where there is very little flow.

Distribution. *G. divergens* is presently known over a broad area of the southern North Island and the northwest of the South Island. A single locality in the Bay of Plenty is known. *G. divergens* has been recorded from the following localities: Tukuhou Stream at Horomanga, Rangitaiki System (Fig. 25: 1*); a tributary of the Mangahao River at Mangamaire, Manawatu River System (2); Bull Stag Creek, Kiriwhakapapa tributary (3*) and Hinaki Stream, a tributary of the Mangatarere Stream (5*), both in the Ruamahanga River System; Mangakotukutuku Stream, Waikanae River System (4*); Hutt River at Kaitoke (6*); Catchpool Stream, Wainuiomata River System (7*); tributary of the Wakamarina Stream, Pelorus River System (8*); tributary of the Motueka River at Golden Downs (9*), and another tributary, the Clarke River at Hope Saddle (10); tributary of Lake Rotoiti (11*, Nelson Lakes); small tributary of Maruia River near Spring's Junction, upper Buller River (12*, type locality).

Galaxias paucispondylus Stokell, 1938
Figure 29

Galaxias paucispondylus Stokell, 1938: 203 (holotype: CMCNZ 73, seen; paratypes (10):

CMCNZ 74, not seen; locality: Acheron River, tributary of the Rakaia River, Canterbury), 1949: 480.

Diagnosis. Differs from *G. divergens* Stokell (Fig. 26) in characters discussed in the diagnosis of that species (p. 384); differs from *G. prognathus* Stokell (Fig. 31) in having fewer anal fin rays, branchiostegals, vertebrae, and gill rakers. It also has a slightly stouter build, longer pectoral fins, and more anterior pelvic fin insertion, but these morphometric differences are rather minor. As with *G. divergens*, *G. paucispondylus* differs from *G. prognathus* chiefly in having sub-equal jaws, this character allowing immediate separation of the two species.

Description. Very elongate and slender bodied, trunk almost square in section, middorsal groove present, indistinct, dorsal and ventral trunk profiles about parallel, with belly somewhat deepened and rounded anterior to the pelvic fins especially in ripe adults; depressed anteriorly on head, somewhat compressed on caudal peduncle, which is very long and slender, much longer than deep. Lateral line a moderate midlateral furrow, accessory lateral line not observed. Head short and tapering, somewhat depressed. Eye small, upper margin near upper head profile, interorbital flat or slightly concave. Lower jaw a little shorter than upper, lips well developed; cleft of mouth extends to about anterior eye margin; profile of lower jaw from ventral aspect broad and shallow, somewhat flattened anteriorly. Canine teeth poorly developed or lacking in jaws; meso-

pterygoidal teeth rather poorly developed; gill rakers variable, weakly to moderately developed, often irregularly spaced with large gaps suggesting loss of rakers; pyloric caeca short.

Dorsal and anal fins somewhat fleshy at bases, short based; greatest fin length somewhat longer than base length, but fins not prominent. Dorsal fin insertion further forward in standard length than in most *Galaxias* (due to the great length of the caudal peduncle); anal origin usually a little behind dorsal origin. Pectoral fin quite small, rounded, inserted moderately high laterally. Pelvic fin short, inserted in front of midpoint of standard length. Caudal fin moderately long, truncated or slightly emarginate, fin depth about equal to greatest body depth, flanges of caudal peduncle moderately developed.

Variation. Meristic: dorsal 7 (3), 8 (10), 9 (36), 10 (9), 11 (1); caudal 15 (3), 16 (54), 17 (1); anal 7 (1), 8 (7), 9 (35), 10 (13), 11 (1); pelvic 6 (14), 7 (43), 8 (1); pectoral 10 (5), 11 (33), 12 (17), 13 (3); branchiostegals 5 (2), 6 (20), 7 (33), 8 (2); vertebrae 50 (2), 51 (10), 52 (18), 53 (9), 54 (1), 55 (0), 56 (1); gill rakers 1–5 (1), 1–6 (3), 1–7 (5), 1–8 (1), 2–6 (7), 2–7 (11), 2–8 (6), 2–9 (1), 3–7 (4), 3–8 (1). Morphometric: see Table 4, p. 387.

Coloration. The basic body color is a grayish cream, interrupted dorsally and laterally by usually bold greenish brown to gray vermiculations. These fail rather high laterally on the belly and caudal peduncle and do not extend much onto the fins except the caudal, which is often quite densely pigmented. The head is heavily pigmented dorsally and also laterally to just below the eyes, but the cheeks, ventral head, and belly are pale, virtually colorless. Quite commonly, this lack of pigmentation on the ventral trunk extends posteriorly beyond the anal fin, even as far as the caudal base. This is unusual in New Zealand galaxiids, in which the lateral trunk pigmentation usually extends as far down

as the anal fin and covers the entire caudal peduncle.

Size. Stokell (1949: 480) recorded *G. paucispondylus* growing to 4.4 inches (112 mm). The largest examined in this study was 104 mm; *G. paucispondylus* commonly grows to 80–85 mm.

Population differences. Samples of *G. paucispondylus* studied came from a restricted area and only three distinct river systems. Samples from only two of these, the Rakaia and Ashburton, were of sufficient size to allow comparison, and the interpretation of inter-population differences is difficult without a series of populations. However, the more southern Stour (Ashburton) population was found to be generally more slender in form than that from the Harper-Avoca-Wilberforce Rivers (Rakaia). In the former, body depth at vent/standard length, head depth/head length, head width/head length, interorbital width/head length, and gape width/head length ratios are all lower (Fig. 30). The meristic data did not show recognizable differences between populations.

Habitat. *G. paucispondylus* occurs only in the swift, cold, snow-fed, boulder-gravel streams of sub-alpine and alpine Canterbury. These rivers tend to be unstable, flood severely with heavy rains and rapid snow thaws, and the rivers wind across broad, flat, open, gravel plains, flanked on either side by steep and often denuded, unstable hills. *G. paucispondylus* is characteristically found in these rivers in the moderately deep, broken-water riffles where the flow is extremely rapid.

Life history. *G. paucispondylus* is restricted to fresh water and has no juvenile whitebait stage. Ripe and spent adults were present together in samples collected in October, suggesting that spawning takes place in the southern spring. However, Stokell (1955: 32) reported that it occurs in March and April. It thus appears that *G. paucispondylus* may have prolonged breeding from spring through the summer to the autumn. The ovaries of fishes
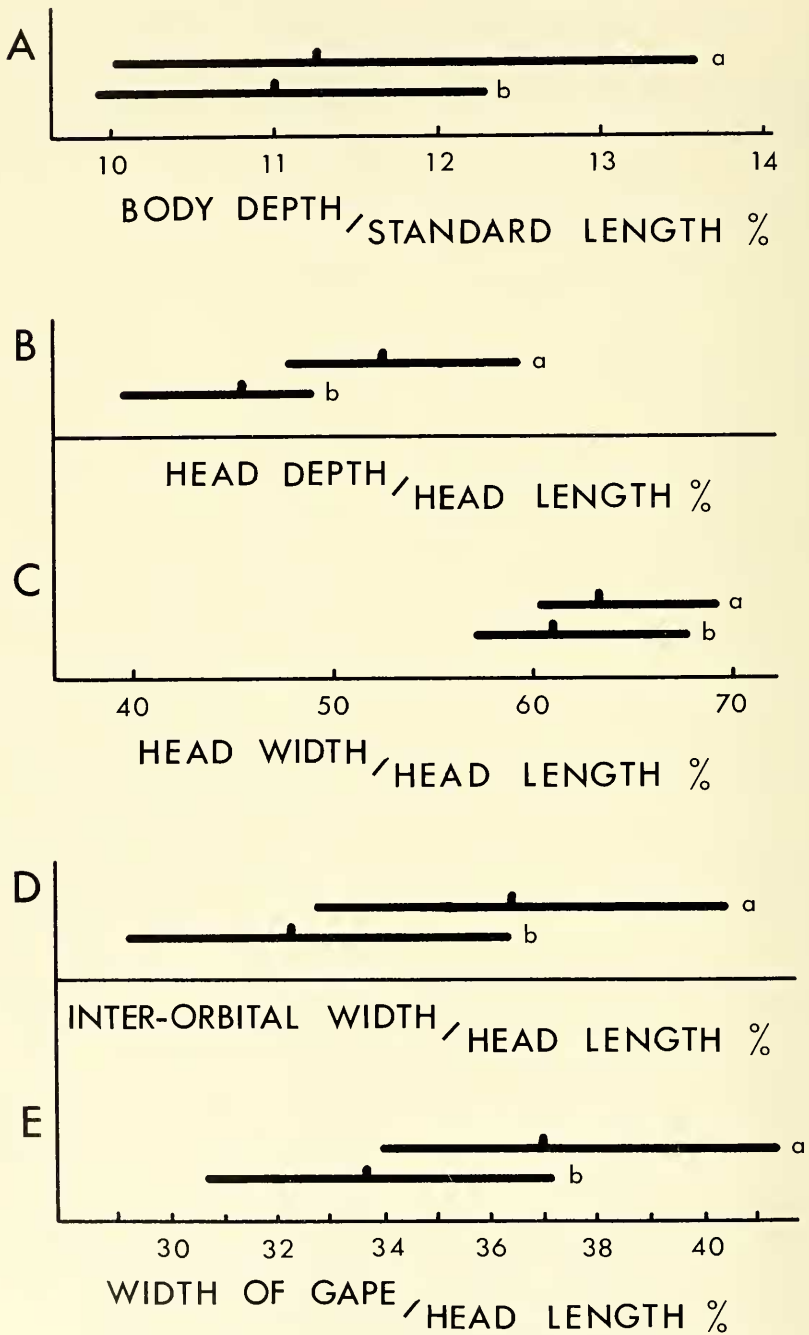
Figure 30.   Variation in body proportions in *Galaxias paucispondylus.* A, Body depth at vent/standard length ratio; B, Head depth/head length ratio; C, Head width/head length ratio; D, Interorbital width/head length ratio; E, Width of gape/head length ratio; a, Rakaia River (15 examples); b, Stour River, Ashburton River System (20 examples).
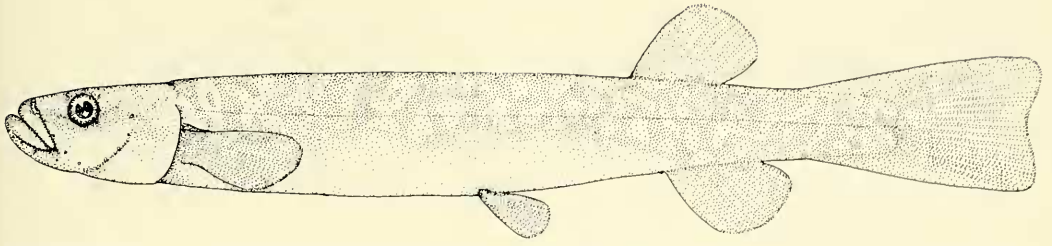
Figure 31. Galaxias prognathus Stokell, 64 mm L.C.F., Avoca River, Rakaia River System.

collected in June were in moderately advanced stages of maturation; others, collected in December, were invariably spent or had very immature ovaries.

The eggs of *G. paucispondylus* are very large, about 2 mm diameter when ripe. They are very few in number, a female 88 mm long having only 269 eggs. The breeding site is unknown to me and is undescribed, but is probably close to the normal adult habitat.

Distribution. G. paucispondylus is presently known only from upland and alpine Canterbury, on the eastern side of the Southern Alps. Populations are known at the following localities: Waimakariri River and its tributaries, the Cass and Porter Rivers (Fig. 25: 14); the Harper, Avoca, Wilberforce (15*), and Acheron Rivers (16) in the Rakaia River System; Stour River, Ashburton River System (17*); Deep Creek, a tributary of the Rangitata River at Mesopotamia Station (18*).

Galaxias prognathus Stokell, 1940
Figure 31

Galaxias prognathus Stokell, 1940: 422 (holotype: CMCNZ 75, seen; locality: Wilberforce River, Canterbury), 1949: 480.

Diagnosis. Differs from *G. divergens* Stokell (Fig. 26) and *G. paucispondylus* (Fig. 29) in characters discussed in the diagnoses of these species (pp. 384 and 390 respectively).

Description. Very elongate and slender in form, belly somewhat rounded and deepened in front of pelvic fins but tapering posteriorly to a slender caudal peduncle, which is very long and much longer than deep. Trunk flattened dorsally with a well-developed middorsal furrow. Lateral line a well-defined midlateral crease; accessory lateral line not observed. Head small and short, tapering considerably, and dorsally flattened; shallow, much broader than deep. Eye small, towards upper head profile, interorbital flat. Lower jaw much longer than upper, upper jaw short, and mouth upturned, lips prominent. Cleft of mouth oblique, usually not reaching anterior eye margin; lower jaw profile from ventral aspect broad and shallow, flattened anteriorly. Canine teeth lacking from jaws; mesopterygoidal teeth weak; gill rakers weak and irregular in development; pyloric caeca lacking.

Dorsal and anal fins showing some basal fleshiness, very short based; greatest fin length somewhat greater than basal length but fins not prominent; distal margin of fins rounded. Dorsal fin insertion well forward, anal origin below or a little behind dorsal origin. Pectoral fin very small and short, somewhat triangular, with the longest rays towards the upper edge of fin, inserted moderately high laterally. Pelvic fin also very small and short, inserted at about midpoint of standard length. Caudal fin moderately long, emarginate to slightly forked, fin depth about equal to body depth. Caudal peduncle flanges showing moderate development, extending about half-way along caudal peduncle to anal fin base.

Variation. Meristic: dorsal 8 (2), 9 (16), 10 (1), 11 (1); caudal 15 (1), 16 (17), 17

(2); anal 10 (13), 11 (7), 12 (1); pelvic 6 (2), 7 (18); pectoral 11 (3), 12 (16), 13 (1); branchiostegals 7 (14); 8 (6); vertebrae 54 (3), 55 (10), 56 (5), 57 (2); gill rakers 1–9 (1), 2–8 (4), 2–9 (9), 2–10 (1), 2–11 (1), 3–9 (1), 3–10 (3). Morphometric: see Table 4, p. 387.

Coloration. Similar to the two preceding species, pale creamish gray with bold, dark, greenish gray vermiculations dorsally and laterally. In a similar manner to the coloration of *G. paucispondylus,* the vermiculations fail rather high laterally, just below the eyes on the cheeks, and not far below the lateral line along the abdomen. The fins are largely colorless.

Size. G. prognathus is known to reach 79 mm length. Fishes 60–70 mm long formed a substantial proportion of a large sample from the Wilberforce River.

Population differences. Since adequate numbers of *G. prognathus* were collected from only one locality, and since all the samples were from the Rakaia River System, no meaningful comparisons of inter-population variation were possible.

Habitat. Like *G. paucispondylus, G. prognathus* occurs in alpine boulder-gravel streams and rivers, and the two species are sometimes taken from the same water. Generally, *G. prognathus* occurs in shallower, turbulent but not broken water. Stokell (1949: 480) reported having collected it mostly in situations where "a side stream rejoins the main stream at such a gradient that the water percolates through the boulders, leaving their upper surfaces dry." In the Wilberforce River, where *G. prognathus* was found to be quite common, the fishes were collected in "shallow riffles up to four inches deep and not particularly fast, but not in the flats," the stream bed composed of "boulders, stones and gravel with considerable silt and sand" (G. A. Eldon, pers. comm.).

Life history. Samples of *G. prognathus* examined were all collected towards the end of October. These fish were mostly spent, although a few were ripe, indicating that spawning was about finished. The eggs are large, about 1.8 mm diameter, and very few in number, a ripe female 68 mm long, with full abdomen, containing only 93 eggs. It is almost certain that the life history is restricted to fresh water, probably in the vicinity of the normal adult habitat.

As was the case with *G. paucispondylus,* my observations are at variance with those of Stokell's (1940: 424, 1955: 34); he reported that spawning occurs in the autumn. However, Stokell's observations were based on a female taken in April with ova measuring only 1.16 mm diameter (1940: 424). My observation of ripe eggs measuring about 1.8 mm suggests that Stokell's fish were not mature. Spawning is probably later in the year than "late autumn or early winter" as suggested by Stokell, and seems likely to occur in the early spring.

Distribution. G. prognathus is known from alpine areas of the central South Island. I have seen samples from the Rakaia River System, the Harper, Avoca, and Wilberforce Rivers (Fig. 25: 15*), and the Maruia River, Upper Buller River System (13). Collections of fishes in the adjacent Waimakariri, Ashburton, and Rangitata Rivers have not contained *G. prognathus.*

NEOCHANNA GÜNTHER

Neochanna Günther, 1867: 306 (type species *Neochanna apoda* Günther, 1867, by original designation).

Diagnosis. Characters generally those of *Galaxias,* but with pelvic fins reduced or lacking; mesopterygoidal teeth reduced or lacking. Jaw teeth sometimes compressed and incisorlike, or conical, as in *Galaxias.* No supraethmoid or ventral ethmoid, vomer folded upwards in front of ethmoid cartilage, ascending processes of premaxillae more or less meeting tips of frontals. No epipleural ribs. Flanges of caudal peduncle very strongly developed, usually confluent anteriorly with dorsal and anal fins.
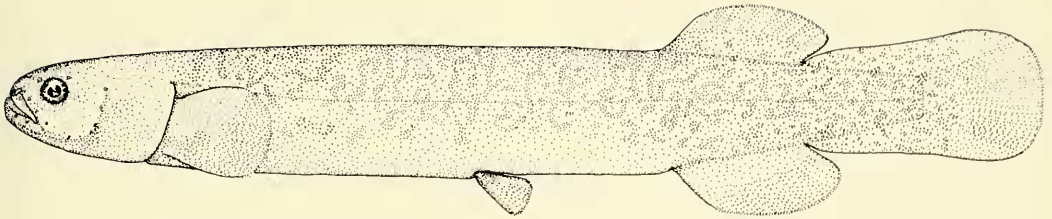
Figure 32.   *Neochanna burrowsius* (Phillipps), 108 mm T.L., Gawler Downs, Hinds River System.

KEY TO SPECIES OF *NEOCHANNA*

1. Pelvic fins present ____ *N. burrowsius* p. 395.
    Pelvic fins absent _____   2.
2. Median fins long, 14–19 rays, D.C.P./
    L.C.P. 129.8–200.0% _____ *N. apoda* p. 398.
    Median fins shorter, 11–16 rays, D.C.P/
    L.C.P. 95.2–135.1% _____ *N. diversus* p. 402.

Neochanna burrowsius (Phillipps, 1926)
Figure 32

Galaxias burrowsius Phillipps, 1926c: 531 (holo-
   type: DMNZ 521, seen; paratype: DMNZ 4646,
   seen; locality: a drain on the farm of the
   late Mr. A. Burrows, West Oxford, Canterbury);
   Stokell, 1949: 481.
Galaxias burrowsii Phillipps, 1927a: 14, 1927b:
   11; Stokell, 1938: 205.
Saxilaga burrowsius: Scott, 1936: 110, 1966: 250.
Paragalaxias burrowsii: Phillipps, 1940: 39.

Diagnosis. Differs from *N. apoda* Gün-
ther (Fig. 34) and *N. diversus* Stokell
(Fig. 36) in the presence of pelvic fins,
and of mesopterygoidal teeth in many
examples; also in the shorter median fins
and lower ray counts in these fins.

Taxonomy. *N. burrowsius* has previously
been included in the genus *Galaxias*, or in
Saxilaga, which has characters intermedi-
ate between *Galaxias* and *Neochanna*. In
its general morphology, it is similar to *N.
apoda* and *N. diversus*, but whereas these
latter species have entirely lost the pelvic
girdles and fins, they persist in *N. bur-
rowsius*. It also often has a few weak meso-
pterygoidal teeth, whereas *Neochanna* is
usually described as having none. (In one
specimen of *N. diversus*, I found a single
tooth on each mesopterygoid.) These
three species have the appearance of a
radiation within the Galaxiidae, comprising

species adapted to temporary creeks and
bogs, which are able to aestivate when
these dry up. They look like a single phylo-
genetic lineage, and their osteology sup-
ports this.

Osteological examination has revealed
characters that indicate close relationship.
In the ethmoid region of the skull, the
three neochannoid species have lost the
supra-ethmoid and ventral ethmoid bones.
The ascending processes of the premaxillae
have become pushed back over the ethmoid
cartilage to meet the anterior tips of the
frontals, and the vomer seems to have been
folded upwards in front of the massive
ethmoid cartilage, above the tip of the
parasphenoid. In *N. burrowsius* and *N.
diversus*, but not in *N. apoda*, the tips of
the ethmoid cartilage, which diverge over
the vomer, each have small tubular ossifi-
cations. In none of the three species are
there epipleural ribs, although all the New
Zealand species of *Galaxias* have them. On
the basis of these considerations, I include
G. burrowsius Phillipps in the genus
Neochanna Günther.

A minor nomenclatural problem exists
in the spelling of the name *burrowsius*. In
his original description, Phillipps (1926c:
531) named the species *G. burrowsius*,
reporting that the fish was collected on the
farm of a Mr. A. Burrows. In later papers
(1927a, b, 1940), he has spelt the name
burrowsii. Mr. Phillipps (pers. comm.)
has kindly advised me that he intended to
name the species for Mr. Burrows, and not
because of its habit of aestivating in small
pockets in mud. The Zoological Code of

Nomenclature is not firm in the formation of patronyms, only recommending (1964: 33, recommendation 31 A) that they should be formed by the addition of "i" to the personal name, if masculine. However, rules for the emendation of name spelling (p. 35, art. 32a) are such that the original spelling must be maintained unless it contravenes mandatory provisions on name formation, or there are obvious, inadvertent errors. Neither of these is the case, so the original spelling must stand. The specific patronym can be regarded as grammatically correct either as an adjective—the Burrows *Galaxias*—or as a noun in apposition.

Numerous attempts to collect *N. burrowsius* from localities listed by earlier workers (Phillipps, 1926c: 532, Stokell, 1949: 482) have failed. The type locality appears to have disappeared as a habitat for *N. burrowsius*, since no creeks or drains could be found at the locality at West Oxford, from which Phillipps first obtained the species (K. F. Maynard, pers. comm.). The present work is based on series collected from localities associated with the Hinds River.

In his description of *N. burrowsius*, Phillipps (1926c: 531) pointed out that teeth were present "only on pre-maxillaries, lower jaw and tongue." Stokell (1945: 129) noted that he had been unable to recollect *N. burrowsius* from the original locality but (1938: 205, 1949: 482) redescribed it from further, new localities. In the later of these papers, he pointed out that teeth may or may not occur on the mesopterygoids. Scott (1966: 250) questioned the correctness of identifying the forms having toothed mesopterygoids with *N. burrowsius*. Since the condition is variable and Phillipps described the species from only two specimens, and since the subsequent collections of fishes included in this species have all been made from a restricted area of Canterbury, there seems little doubt that Stokell's action is correct and that the "neochannoid" species present

in swamps and drains in Canterbury Province, in the vicinities of Ashburton and Christchurch, is *N. burrowsius* (Phillipps).

Description. Trunk much elongated and cylindrical, flattened dorsally with a deep middorsal furrow, dorsal and ventral trunk profiles parallel; little depressed on head, compressed on caudal peduncle, which is of moderate length and depth. Lateral line indistinct anteriorly, becoming a well-defined furrow posteriorly; accessory lateral line present, but weakly developed. Head rounded and blunt, cylindrical. Eye very small, deep set in head, with interorbital convex. Jaws very short, about equal or lower a little shorter, cleft of mouth extends to about anterior eye margin; profile of lower jaw from ventral aspect somewhat deep and narrow, a broad U. Canine teeth lacking in jaws; mesopterygoidal teeth poorly developed and few in number, or lacking. Gill rakers short; pyloric caeca well developed.

Median fins short based and low, with well-developed basal fleshiness. Overall fin length little greater than basal length, distal margins of fins more or less straight and tending to become parallel with trunk axis. Predorsal length moderate, anal origin usually below or a little behind dorsal origin. Pectoral fin very short, rounded, inserted moderately high laterally; pelvic fins much reduced, inserted at about midpoint of standard length. Caudal fin short and much rounded, fin depth about equal to body depth; caudal peduncle flanges very strongly developed and extending forwards to the insertions of the dorsal and anal fins, more or less confluent with posterior ends of their bases.

Variation. Meristic: dorsal 7 (1), 8 (11), 9 (14), 10 (5), 11 (3); caudal 11 (2), 12 (1), 13 (20), 14 (12); anal 8 (4), 9 (15), 10 (10), 11 (5), 12 (1); pelvic 4 (1), 5 (14); pectoral 10 (1), 11 (10), 12 (3); branchiostegals 5 (1), 6 (9), 7 (3); vertebrae 51 (2), 52 (6), 53 (16), 54 (7), 55 (1); gill rakers 2–9 (1), 2–10 (1), 3–8 (1),
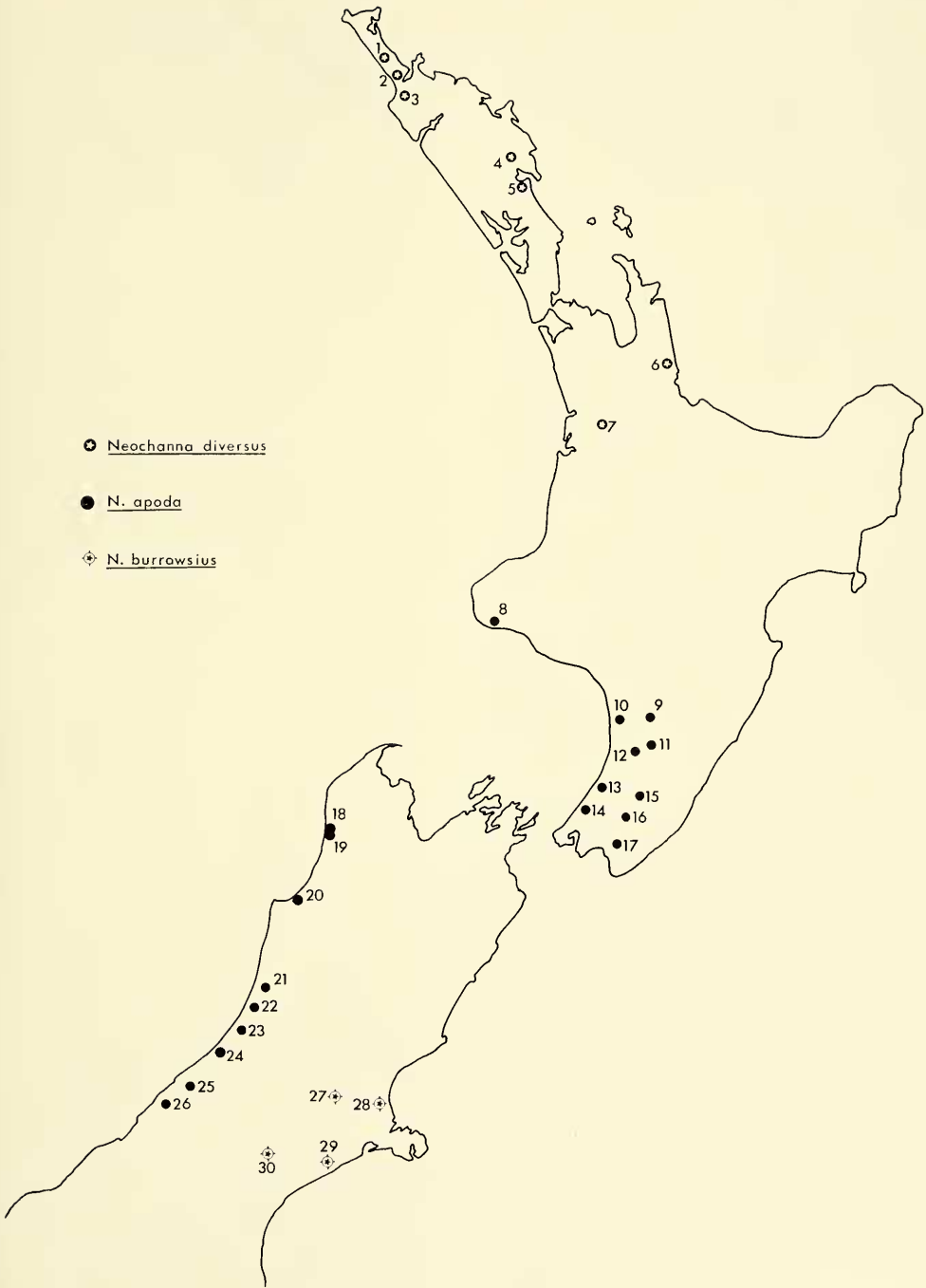
Figure 33. Distribution of *Neochanna burrowsius*, *N. apoda*, and *N. diversus* (numbers in figure as in text pp. 398, 402, and 404).
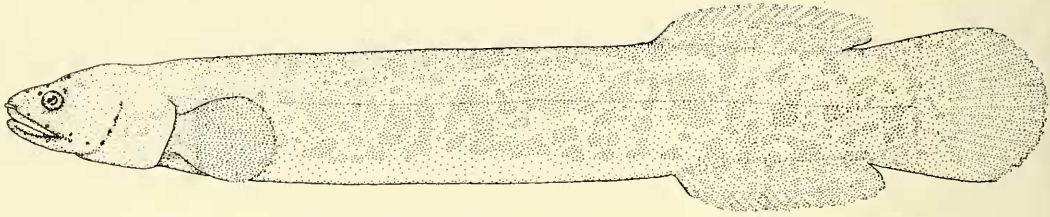
Figure 34. *Neochanna apoda* Günther, 110 mm T.L., tributary of Mangatarere Stream, Ruamahanga River System

3–9 (2), 3–10 (5), 3–11 (2), 3–12 (1), 4–9 (2), 4–10 (2), 4–11 (3). Morphometric: see Table 5, p. 399.

Coloration. Trunk a milky gray-brown, covered dorsally and laterally with fine, darker, greenish brown vermiculations, these extending well on to the fin bases. Belly paler, a milky brown.

Size. An example from the Anama sample measured 146 mm total length. Amongst the few fish examined, a good proportion were 100–125 mm long.

Population differences. Unfortunately, all the specimens examined were collected from the Hinds River System, in the same restricted area, so that no investigation of differences between populations was possible.

Habitat. N. burrowsius appears to be collected usually from small, muddy, or gravel-bed streams and creeks, often those draining swamps. Phillipps (1926c: 532) reported their ability to aestivate in small pockets of mud in the same manner as other *Neochanna* species are well known to do. Stokell (1949: 482) also reported specimens dug out of "damp earth and detritus at the bottom of a drain that had been dry for over a month."

Life history. N. burrowsius collected from the Hinds River System in early August were approaching maturity. All those taken in November were spent. Thus *N. burrowsius* probably spawns in the spring. No females from the August sample were sufficiently mature to permit egg counts or measurements, but egg number appeared to be moderately high, perhaps comparable with that of *G. macu-*

latus. There is no whitebait stage and no obvious juvenile-adult metamorphosis, and it is almost certain that *N. burrowsius* spends all its life in fresh water.

Distribution. N. burrowsius is known only from the Canterbury District, South Island. It has been collected from the following localities: West Oxford (Fig. 33: 27, type locality, Phillipps, 1926c: 532); Rangiora (28) and Tinwald (29, Stokell, 1949: 482); Gawler Downs, Anama District, Hinds River (30*).

Neochanna apoda Günther, 1867
Figure 34

Neochanna apoda Günther, 1867: 306 (holotype: BMNH 1965.11.5.8, not seen; locality: "near Hokitika," west coast, South Island); Hector, 1869: 402; Hutton, 1872: 61; Vollams, 1872: 456; Hutton, 1904: 51; Regan, 1905: 383; Phillipps, 1923: 62, 1926b: 297, 1927a: 14, 1940: 41; Stokell, 1949: 494.

Diagnosis. Differs from *N. burrowsius* (Phillipps) (Fig. 32) in characters discussed in the diagnosis of that species (p. 395); differs from *N. diversus* Stokell (Fig. 37) in having longer dorsal and anal fin bases, a much shorter caudal peduncle, a broader head, smaller eyes, and much longer jaws. It also has more rays in the dorsal and anal fins, more branchiostegals and, particularly in the southern part of its range, fewer vertebrae. *N. apoda* has much paler coloration than *N. diversus*.

Description. Trunk elongated and somewhat rounded, middorsal furrow prominent; dorsal and ventral trunk profiles about parallel; head little depressed anteriorly, caudal peduncle much compressed and thin posteriorly, short, much

TABLE 5. MORPHOMETRIC VARIATION IN THE "NEOCHANNOID" SPECIES (FIGURES GIVEN AS PERCENTAGES OF DENOMINATOR OF RATIO).

	N. burrowsius			N. apoda			N. diversus		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./T.L.	87.0	89.3	91.7	85.5	88.5	90.9	88.5	90.9	92.6
B.D.V./S.L.	10.0	11.0	11.9	10.4	12.9	14.9	10.5	11.9	15.0
L.C.P./S.L.	11.6	12.8	15.2	4.9	6.5	7.8	8.5	10.2	12.9
D.C.P./L.C.P.	56.8	64.9	76.9	129.9	158.7	200.0	95.2	11.2	13.5
Pre D./S.L.	69.4	73.5	76.3	69.9	72.5	75.8	71.4	74.1	76.9
Pre D./Pre A.	94.3	98.0	101.0	93.5	97.1	101.0	97.1	101.0	105.3
D.F.B./S.L.	9.7	11.6	14.0	19.3	21.9	25.3	10.1	13.8	16.3
D.F.B./D.F.M.	59.9	71.9	84.0	75.2	83.3	90.9	69.4	78.7	92.6
A.F.B./S.L.	10.5	13.1	15.8	20.2	22.4	25.8	16.7	18.9	20.8
A.F.B./A.F.M.	69.9	80.7	87.0	78.1	86.2	96.2	84.8	90.9	98.0
Pre Pel./S.L.	48.9	51.3	53.8	—	—	—	—	—	—
Pec.Pel./S.L.	29.0	34.0	36.1	—	—	—	—	—	—
Pec./Pec.Pel.	24.1	27.3	36.4	—	—	—	—	—	—
Pel.An./S.L.	20.3	23.6	27.1	—	—	—	—	—	—
Pel./Pel.An.	23.1	29.1	35.8	—	—	—	—	—	—
H.L./S.L.	16.7	18.4	20.2	18.5	21.2	24.2	18.6	20.1	21.8
H.D./H.L.	46.5	53.8	59.2	44.4	52.9	59.2	42.4	49.8	58.5
H.W./H.L.	52.1	59.5	64.1	56.8	62.9	71.9	53.8	59.9	65.8
Sn.L./H.L.	22.4	27.5	31.9	23.8	27.0	29.8	25.6	27.9	31.3
P.O.H.L./H.L.	54.6	59.5	63.3	57.1	63.7	70.4	58.8	62.9	68.5
Io.W./H.L.	32.8	36.1	40.0	32.6	36.8	42.7	35.5	39.1	45.1
D.E./H.L.	10.3	12.5	15.3	8.3	11.2	15.5	11.1	13.0	15.6
L.U.J./H.L.	27.6	31.3	33.3	36.2	39.7	44.1	27.0	30.4	32.3
L.M./H.L.	28.0	30.7	35.1	34.7	38.8	43.1	30.0	31.6	32.3
W.G./H.L.	34.5	38.0	42.4	36.1	41.7	50.0	30.8	35.2	38.3
Pec./H.L.	—	—	—	42.4	53.3	62.1	45.2	50.6	56.8
Fish examined		21			38			16	

deeper than long. Lateral line a deep lateral groove; accessory lateral line present. Head moderately long, broader than deep, somewhat bulbous behind nape, and tapering abruptly from just behind eye forwards on to a rather slender snout. Eye very small, deep set in head, with interorbital convex. Jaws about equal, very long, cleft extending well below eye, about as far as posterior eye margin. Gape very broad, profile of jaw from ventral aspect quite deep but moderately broad, somewhat flattened anteriorly. Canine teeth lacking from jaws; jaw teeth peculiarly compressed and incisorlike; mesopterygoidal teeth lacking; gill rakers moderate to short; pyloric caeca strongly developed.

Unpaired fins low, but very long based, with much basal fleshiness; greatest fin length little greater than basal length, distal margin of fin straight, parallel to trunk axis; fin bases confluent posteriorly with caudal peduncle flanges. Anal origin usually a little behind dorsal origin. Pectoral fin short, rounded, insertion high laterally. The fins all show coarse marginal serration.

Variation. Meristic: dorsal 14 (2), 15 (10), 16 (4), 17 (14), 18 (5), 19 (2); caudal 13 (1), 14 (5), 15 (11), 16 (16), 17 (3); anal 14 (2), 15 (6), 16 (9), 17 (10), 18 (4), 19 (6); pectoral 11 (2), 12 (15), 13 (20); branchiostegals 6 (12), 7 (19), 8 (5), 9 (1); vertebrae 52 (5), 53 (9), 54 (3), 55 (5), 56 (6), 57 (3), 58 (2), 59 (2); gill rakers 1–9 (1), 2–8 (18), 2–9 (12), 3–8 (7), 3–9 (4), 4–9 (1). Morphometric: see Table 5.

Coloration. Trunk usually sandy colored, darker dorsally, with the usual
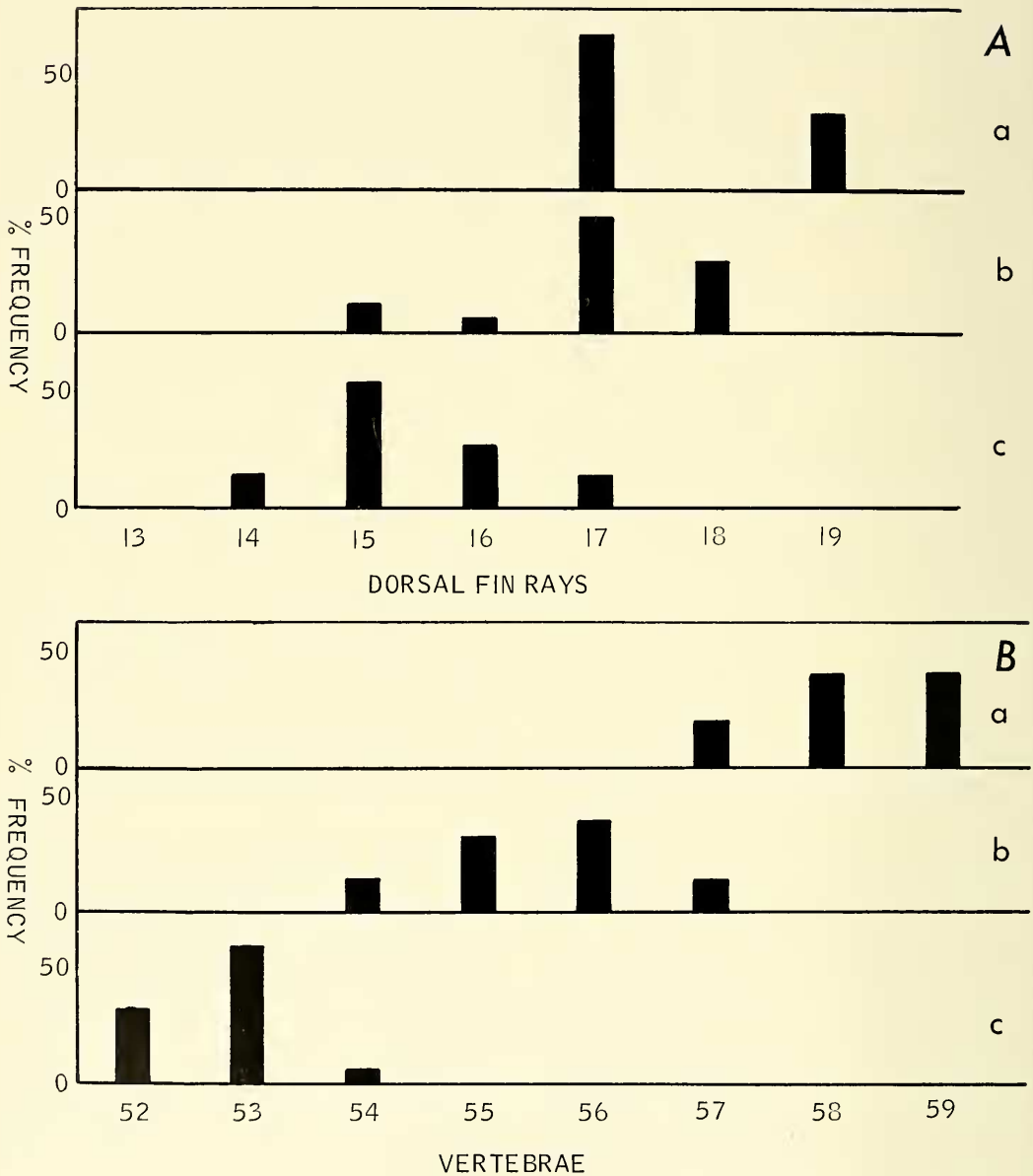
Figure 35. Variation in meristics in *Neochanna apoda.* A, Dorsal fin rays; B, Vertebrae; a, Wellington District (8 examples); b, Wairarapa District (20 examples); c, Western South Island—Westland District (13 examples).

irregular darker vermiculations of green-ish brown color. Coloration much browner than most galaxiids in New Zealand, which are usually brownish gray to a deep purplish brown. Belly a pale cream-buff color. Fin bases well pigmented with vermiculations as on trunk. Samples from the west coast of the South Island were generally somewhat darker than northern ones, with the vermiculations tending to

become resolved into rather bold, broad, dark, vertical bands.

Size. Stokell (1949: 494) recorded *N. apoda* growing to 6.8 inches (173 mm). The largest example examined in the present study was 169 mm long. *N. apoda* appears commonly to reach 100–130 mm.

Population differences. *N. apoda* exhibits wide variation in meristic and some morphometric characters. Unfortunately, only two populations were available of sufficient size to allow adequate comparisons to be made. However, by grouping samples it was possible to compare data from three major, discrete areas. These were the Wairarapa, the Wellington Province west of the main ranges, and the west coast of the South Island. The number of specimens from the Wellington area (five) is totally inadequate for definitive comparisons, but these few specimens showed substantial, interesting differences from the others. Vertebral number was found to be greatest in Wellington fishes, somewhat lower in those from the Wairarapa, and minimal in those from the west coast of the South Island (Fig. 35B). Dorsal (Fig. 35A), anal, and caudal fin ray counts showed a similar trend; the greatest number of fin rays was found to occur in the more northerly populations. These data appear to be contrary to clines related to water temperatures, in which the populations in warmer areas would be expected to have fewer elements, unless there is something peculiar about the temperatures of water bodies from which these populations were collected. The variation in caudal fin rays is interesting in that this is otherwise by far the least variable of any of the meristic characters in the family. Branchiostegal number showed a different trend from other counts, being least in the Wairarapa samples and greatest in west coast samples, the Wellington fishes occupying an intermediate position.

The head length/standard length ratio of the Wellington fishes was much lower
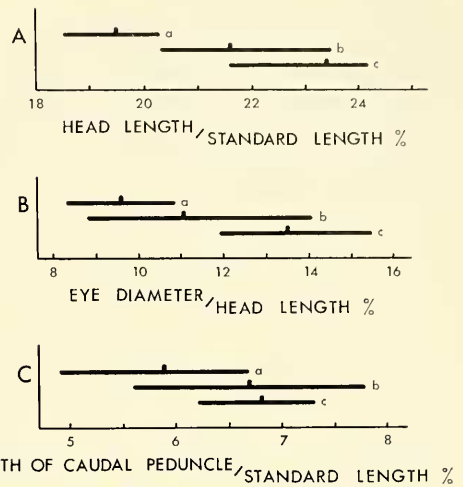
Figure 36. Variation in body proportions in *Neochanna apoda*. A, Head length/standard length ratio; B, Eye diameter/head length ratio; C, Length of caudal peduncle/standard length ratio; a, Wellington District (8 examples); b, Wairarapa District (23 examples); c, Western South Island—Westland District (8 examples).

than that of those from the Wairarapa, in which the ratio was lower than those from the west coast. Eye diameter exhibited similar variability. The length of the caudal peduncle was similar in Wairarapa and west coast material but greatly decreased in the few Wellington specimens examined (Fig. 36).

This variability appears to generate no clear pattern and it is obviously necessary to await collection of more material, especially from the western part of the Wellington province, before these differences can be understood. Eventually it may be necessary to divide what is here treated as a single species at either the species or sub-species level.

Habitat. In the Wairarapa, *N. apoda* has been usually collected in the upper reaches of small, spring-fed creeks, often filled with bottom-rooted vegetation. On the west coast of the South Island it was found in the tannin-stained waters of bush swamps, under a heavy forest cover, and in streams flowing into flax swamps. *N. apoda* is typical of the New Zealand mud-fishes in

its ability to withstand desiccation of its habitat. G. A. Eldon (pers. comm.) reported collecting one specimen from beneath a log in the middle of a partially cleared cow pasture, with no water near by at the time of capture. Phillipps (1923: 62) reported that it was collected from white pine swamps, and Reid (1886) reported that healthy *N. apoda* had been collected five or six feet down in clay, suggesting that the fishes follow moisture down holes left by rotted tree roots. Stokell (1955: 38) also mentioned its ability to bury itself in mud in times of drought.

Life history. Little is known of the life history of *N. apoda.* Stokell (1949: 495) noted that males taken in October "had the milt almost fully developed and appeared to be within a week or two of spawning." Davidson (n.d.) found that Wairarapa *N. apoda* spawn "probably . . . not before the end of November." A specimen taken in June by Phillipps (1926b: 297) is reported to have been in spawning condition. Material collected from the west coast of the South Island in late October was all apparently recently spent, or in the early stages of gonad rejuvenation, whilst the sample from the Kaipaitangata System (Wairarapa) collected in February contained a mixture of ripe and spent individuals. It appears that at present, no clear breeding period for *N. apoda* can be defined; it is possibly of long duration.

The eggs of *N. apoda* are moderately large, about 1.75 mm diameter, and few in number. A female from the Wairarapa, 115 mm long, contained only 533 eggs. Growth of juveniles is almost certainly in or near the adult habitat, as examples only 27 1/2 mm long were collected with adults. They are, at this small size, similar in form and coloration to the adults.

Distribution. *N. apoda* is found in the south of the North Island and on the west coast of the South Island. It is known from the following localities: Opunake

(Fig. 33: 8); Feilding (9, Davidson, n.d.); Rangitikei (10, Phillipps, 1923: 62); Palmerston North (11, Stokell, 1949: 494); Rongotea (12*); Otaki (13*); Waikanae (14*); Masterton (15, Phillipps, 1926b: 297); tributary of the Kaipaitangata stream, Ruamahanga River System (16*); tributary of Lake Wairarapa at Pirinoa (17*); Oparara (18); Birchfield (19); Westport (20, Eldon, 1968); Greymouth (21, Stokell, 1949: 494); Kumara Junction (22*); Hokitika (23*); Ross (24, Eldon, 1968); Harihari (25*); Whataroa (26*).

Neochanna diversus Stokell, 1949
Figure 37

Neochanna diversus Stokell, 1949: 495 (holotype: CMCNZ 76, seen; locality: Kaitaia, North Auckland).

Diagnosis. Differs from *N. burrowsius* (Phillipps) (Fig. 32) and *N. apoda* Günther (Fig. 34) in characters noted in the diagnoses of these species (pp. 395 and 398 respectively).

Description. Rather slender bodied, trunk rounded in section without middorsal furrow; dorsal and ventral trunk profiles parallel from about head to dorsal origin, although the belly deepens noticeably in ripe adults. Trunk much compressed posteriorly on caudal peduncle, but little depressed anteriorly on head. Caudal peduncle deep and relatively long. Lateral line indistinct, accessory lateral line present. Head short, very blunt, broader than deep; head profile smooth and rounded, snout profile very convex. Eye very small, set deep in head, interorbital very convex. Jaws short, about equal, or lower protruding slightly; cleft of mouth reaching below anterior half of eye, oblique. Profile of jaw from ventral aspect rather broad and flattened anteriorly. Jaw teeth conical, lacking canines, usually no mesopterygoidal teeth, although one fish with one tooth on each mesopterygoid was observed. Gill rakers variable in length, from moderately to well developed; pyloric caeca also variable, usually moderately developed.
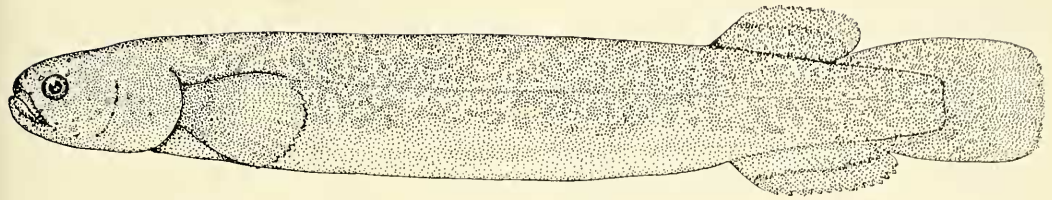
Figure 37.   *Neochanna diversus* Stokell, 112 mm T.L., swamp at Waiharara, North Auckland District.

Median fins moderately long based and expansive, but extending little along caudal peduncle beyond end of fin base, extremely fleshy basally, fleshiness failing on distal half of fin, which is quite membranous; margins of fins straight, more or less parallel to trunk axis. Anal origin at or a little in advance of dorsal origin. Dorsal and anal fins confluent with caudal peduncle flanges, which are very strongly developed. Caudal fin short, moderately fleshy at base, truncated to rounded. Pectoral fin short, membranous or slightly fleshy, rounded, inserted high laterally. Margins of fins serrate.

Variation. Meristic: dorsal 10 (2), 11 (4), 12 (7), 13 (21), 14 (2); caudal 15 (6), 16 (25), 17 (5); anal 13 (4), 14 (5), 15 (19), 16 (4); pectoral 11 (1), 12 (14), 13 (17), 14 (4); branchiostegals 6 (12), 7 (24); vertebrae 55 (2), 56 (9), 57 (7), 58 (12), 59 (10), 60 (2); gill rakers 2–8 (5), 2–9 (3), 3–8 (8), 3–9 (14), 3–10 (6), 4–8 (2), 4–9 (3), 4–10 (1). Morphometric: see Table 5, p. 399.

Coloration. Dark colored; in populations examined from peat bogs, a dark smoky gray to almost black; profuse fine vermiculations cover the dorsal and lateral trunk and the fin bases. The belly is paler, smokey gray to somewhat rufous.

Size. An example from the Waiharara series measured 122 mm total length. Samples contained few examples more than 90 mm long.

Population differences. Noticeable differences in meristics were found for the two large samples of *N. diversus* examined.

The Waiharara sample (the more northern locality) was found to have generally fewer counted structures, especially vertebrae, anal fin rays, and gill rakers. The sample from the most southern locality, Mount Pirongia, included only four fish, but these appeared to be more similar to those of the Waiharara series than to that from the Hikurangi swamp (e.g., vertebral number, Fig. 38). In the Waiharara and Hikurangi samples, ranges for anal fin rays and gill raker counts showed decided displacement from each other, and vertebral number was almost disjunct in the two samples (although the Hikurangi distribution is noticeably skewed). Thus, as was the case with *N. apoda*, differences between samples from highly isolated localities appear to be considerable. Collections of samples from further, intermediate localities and at-
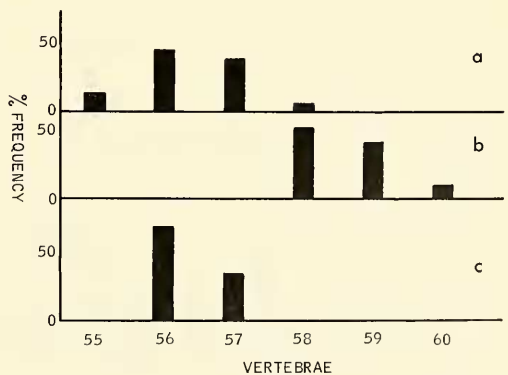

Figure 38.   Variation in vertebral number in *Neochanna diversus*. a, Waiharara, North Auckland District (16 examples); b, Hikurangi, North Auckland District (22 examples); c, Mt. Pirongia, Waikato District (3 examples).

tempts to relate water temperatures or other ecological parameters to morphological characters may prove worthwhile.

Habitat. Stokell (1949: 495) discussed the habits of *N. diversus*, reporting that one of his specimens came from the mud of a creek in the summer, and that six were taken, free-swimming, during the winter. In March, 1965, several days were spent in the vicinities of Mt. Pirongia, Kaitaia, and Whangarei searching for this species in muddy creeks and drains, without success except at Mt. Pirongia. Only three specimens were found (the fourth was obtained from a local farmer). At Waiharara, one of the creeks searched unsuccessfully was a narrow channel draining a substantial shallow lagoon. Near this lagoon is a large area of Kauri-gum swamp, in which there are many small depressions, a few inches to several feet across and up to 18 inches deep. When examined, most of the holes were heavily overgrown with sphagnum, and often filled with twigs to the extent that they were scarcely distinguishable from the surrounding peat. It was here that *N. diversus* was found. By moving from hole to hole, clearing away the sphagnum and debris, waiting for the sediment to clear, and fishing in each with the electric fishing machine, it was found that each hole usually contained two or three fishes. Collections from the Hikurangi swamp, near Whangarei produced *N. diversus* from similar habitats. It appears, then, that these holes, rather than the streams running through swamps or draining them, are the characteristic habitat of *N. diversus*.

Life history. Mature, adult *N. diversus* were present in the samples collected from the North Auckland area in March. A single example from the vicinity of Waihi, collected in January, contained ovaries at an early stage of maturation. Stokell (1949: 495) found that examples collected from Kaitaia at the end of July were fully ripe or partly spent. These data indicate that *N. diversus* probably breeds during the winter. This is reasonable for a species that lives in a habitat that may dry up in the summer and that is known to be able to aestivate when this occurs.

The eggs of *N. diversus* are moderately large, those from the most mature female in the collection being about 1.6 mm diameter. These were not ripe; the fully ripe eggs may be somewhat larger. Corresponding with their size, they were found to be rather few in number, only 940 being present in a female 119 mm long.

Distribution. *N. diversus* was recorded by Stokell (1949: 495) from Waihopo (Fig. 33: 1), Kaitaia (3), and Mangawai (5). An example in the collection of the New Zealand Dominion Museum is from Waihi (6*); in the present study additional specimens were collected from Waiharara (2*); the Hikurangi Swamp at Whakapara (4*); Mt. Pirongia (7*). These localities suggest that it has a general distribution in swamplands in the Auckland Province, as far south as Waihi and Mt. Pirongia.

SPECIES *INCERTAE SEDIS*

Galaxias kaikorai Whitley

Galaxias kaikorai Whitley, 1956c: 34 (holotype: GMUO 6330–1; locality: Fraser's Gully, Kaikorai, near Dunedin, late Pliocene diatomaceous shale).

Taxonomy. Whitley applied this name to a fossil collected from a Pliocene freshwater deposit in southeastern New Zealand. Stokell (1945) examined this fossil thoroughly, concluding that it belongs in the genus *Galaxias*, but that it is probably not conspecific with living species. Whitley (1956) supplied no diagnostic characters for the species, and its validity is undetermined, but since the name was referred to a specimen and a partial description, the name has taxonomic standing. I have not examined the fossil and believe that further similar fossils have recently been discovered at the same locality (P. M. Johns, pers. comm.). Examination of these fossils may help to clarify the situation.
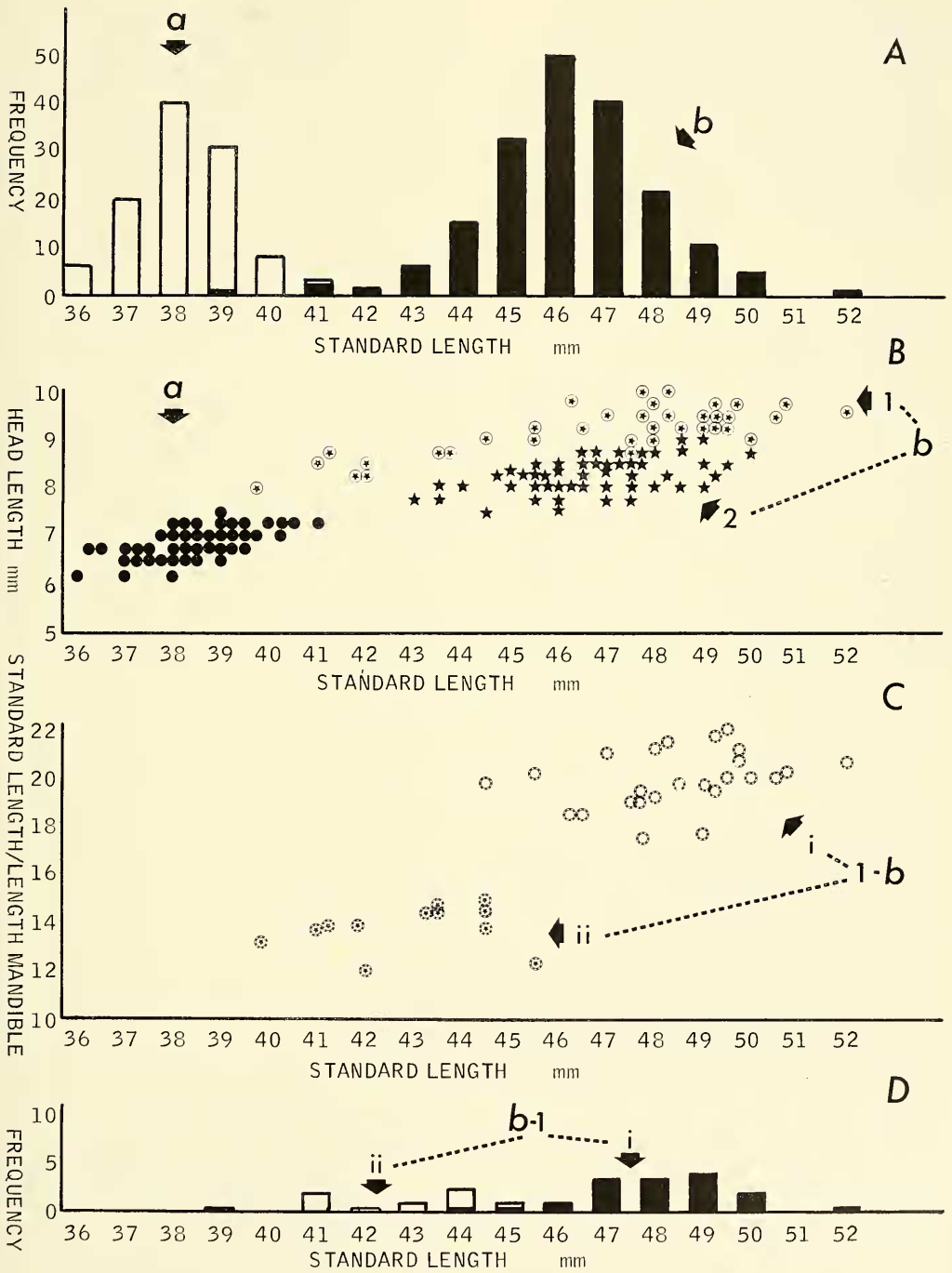
Figure 39.   Identification of juveniles of diadromous New Zealand galaxiids (explanation of symbols in text, pp. 406–408).

Galaxias abbreviatus Clarke

Galaxias abbreviatus Clarke, 1899: 80.

Nomen nudum. This name was used by Clarke in a discussion of the *Galaxias* species of the west coast of the South Island. The origin of the name is unknown; it does not occur in earlier literature, and Clarke applied it to no description or type.

DISCUSSION

Identification of diadromous whitebait juveniles

The juveniles of the diadromous species of *Galaxias* in New Zealand lack many of the diagnostic characters of their respective adults, e.g., definitive pigmentation and dentition, and body proportions are very different from those of the adults. Overlapping meristic values for the five species also add to the difficulties of identification. Because of this, the species are difficult to distinguish (McDowall, 1964b: 142, 1965a). In my 1964 study, *G. fasciatus* and *G. postvectis* were not properly separated, and Woods (1966: 177) succeeded in identifying only three of the five species occurring in the rivers of the west coast of the South Island.

In New Zealand, *G. argenteus*, *G. fasciatus*, *G. postvectis*, *G. brevipinnis*, and *G. maculatus* have whitebait juveniles (McDowall, 1966a: 13). In earlier studies, samples were collected from the Buller River (Westland) and rivers nearby, and the four species, in addition to *G. maculatus*, were identified by rearing the fishes. The samples preserved at that time have been re-studied and the results are presented here.

The whitebait of *G. maculatus* (Fig. 40) is easily identified by its very bold pigmentation. The lateral line is very clearly defined by a series of large melanophores (which are small or lacking in other species), and there are several to many very large melanophores on the dorsal trunk anterior to the dorsal fin. In other species

these melanophores are lacking. More objective characters that distinguish the whitebait of *G. maculatus* include its low pectoral fin ray number (11–15, usually 12–13), combined with high anal fin ray counts (14–18, usually 15–17).

After eliminating *G. maculatus* whitebait from samples, a length-frequency histogram of the remaining fishes showed that there were two very different size categories (Fig. 39A, a and b); these suggest size difference for some species at migration. A plot of standard length against head length indicated the same division of the samples (Fig. 39B, a and b). Further study of the fishes in the smaller size range (Fig. 39A, a) showed them to comprise only one species, and from much experience in collecting and studying these fishes, and having studied series of developmental stages from freshly migrated juveniles to fully pigmented sub-adults, I am quite confident that they are the whitebait of *G. fasciatus* (Fig. 41).

By elimination, the fishes in the larger size group (Fig. 39A, b) comprised a mixture of *G. argenteus*, *G. postvectis*, and *G. brevipinnis*. The adults of the first two species are much stouter than that of the third, and this difference is also evident in the juveniles. A plot of standard length against body depth at vent enabled division of the fishes into two somewhat overlapping groups, and the same division was produced in a plot of standard length against head length (Fig. 39B, b, 1–2). Examination of the fishes showed that the more slender ones (b, 2) also had a much shorter-based anal fin than the stout fishes, and that the anal fin origin was set further back from the dorsal origin. These two subjective characters enabled me to place the fishes in the overlap zone between the two major groupings, in the appropriate group. The slender fishes, from the slenderness, the short anal fin set back from the dorsal fin, and again from examination of developmental series, are the whitebait juveniles of *G. brevipinnis* (Fig. 42).
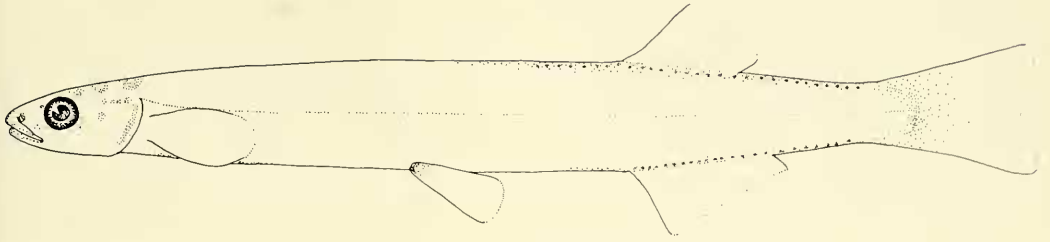
Figure 40. Whitebait juvenile of *Galaxias maculatus* (Jenyns), 53 mm L.C.F.
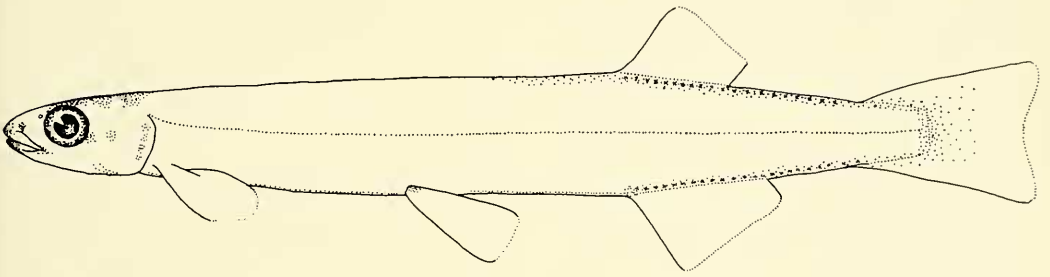

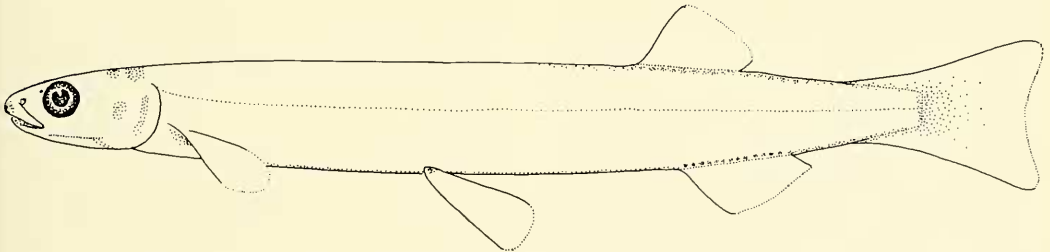Figure 41. Whitebait juvenile of *Galaxias fasciatus* Gray, 48 mm L.C.F.

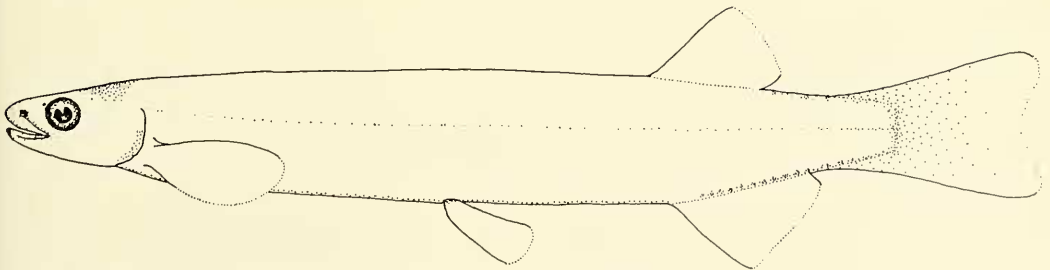Figure 42. Whitebait juvenile of *Galaxias brevipinnis* Günther, 50 mm L.C.F.

Figure 43. Whitebait juvenile af *Galaxias argenteus* (Gmelin), 50 mm L.C.F.
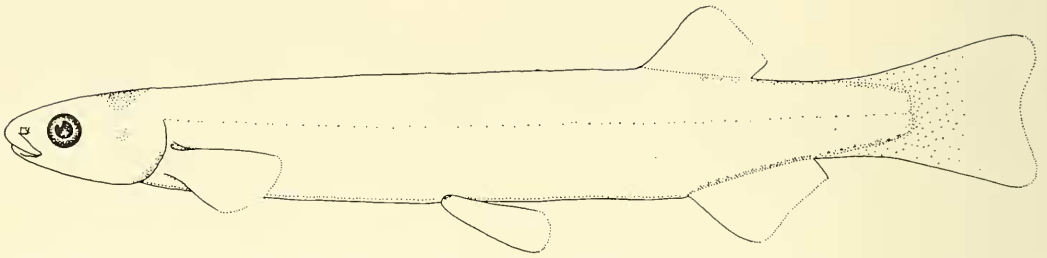
Figure 44.   Whitebait juvenile of *Galaxias postvectis* Clarke, 54 mm L.C.F.

The remainder of the samples, containing the larger and stouter fishes, consisted of *G. argenteus* and *G. postvectis* (Fig. 39C), and these fishes could be separated on the basis of standard length (Fig. 39D). The adult of *G. postvectis* has a distinctly receding lower jaw, whereas in *G. argenteus* the jaws are about equal; this character enabled the identification of those fishes with the receding lower jaw as *G. postvectis* (Fig. 44), and the shorter ones with the lower jaw not receding, as *G. argenteus* (Fig. 43). I am fairly confident that the groups divided and identified by this procedure are correct, but the only way to confirm this appears to be further rearing trials.

This study has not isolated particular characters by which individual specimens of the four problematical species can be identified with any assurance. But it does show that it is possible to separate the species when they occur in mixed-species samples. In addition, the experience of carrying out this sorting procedure highlights the subjective characteristics of the whitebait of each species, and with this experience, it becomes possible to sort the species more directly. If this procedure can be carried out on a large scale, it will be possible to analyze seasonal differences in migratory patterns and the various ecological parameters which, in differing ways, influence the migrations of each of the species. Such an analysis would constitute significant progress towards understanding and intelligently managing the fishery.

In Table 6, the ratios for head length/standard length and body depth at vent/standard length of juveniles and adults of each of the five diadromous species in New Zealand are listed. These data show that in all the species, the head becomes proportionately much longer and the body

TABLE 6. BODY PROPORTIONS OF DIADROMOUS GALAXIIDAE.

		Head length as % of standard length			Body depth at vent as % of standard length			Fish examined
		Min.	Mean	Max.	Min.	Mean	Max.	
G. argenteus	Juvenile	19.6	20.0	21.2	11.9	12.8	14.0	6
	Adult	27.0	29.1	30.5	18.7	21.0	23.4	36
G. fasciatus	Juvenile	16.4	17.8	18.8	10.5	11.8	13.2	151
	Adult	22.8	25.9	28.6	15.0	17.9	21.4	60
G. postvectis	Juvenile	18.0	19.4	21.1	11.7	12.6	14.9	16
	Adult	21.2	23.0	25.0	16.4	19.6	22.4	25
G. brevipinnis	Juvenile	16.3	17.8	18.8	10.0	11.1	12.2	186
	Adult	20.6	23.6	28.7	11.0	13.2	15.3	160
G. maculatus	Juvenile	12.4	14.5	16.1	8.8	9.4	11.2	40
	Adult	18.5	20.0	21.6	10.3	11.6	12.9	40

deeper during growth. I have shown elsewhere (McDowall, 1968b) that in *G. maculatus,* the change in head length/standard length ratio is a result of trunk shrinkage just after migration, but I have insufficient material of the other species to determine whether this occurs in them also.

Life history and distribution patterns

Two distinct life history patterns are recognizable in the New Zealand Galaxiidae. Five species, *G. maculatus, G. brevipinnis, G. fasciatus, G. postvectis,* and *G. argenteus* have numerous, small to moderate-sized eggs, they spawn mostly in the autumn or early winter, and the freshly hatched larvae are carried to sea and undergo juvenile development there. About six months later, in the following spring, the slender, transparent whitebait juveniles, 40–55 mm long, migrate upstream in large, mixed-species shoals, undergo a minor metamorphosis, become pigmented, and assume adult form. In four of these species, the sub-adults become solitary in habit and are usually found in stream cover of some variety. The caudal fin changes from forked to emarginate or truncated, and all the fins become thick and fleshy, especially basally.

In contrast, the adult of *G. maculatus* retains the shoaling habits, the forked caudal, and membranous fins of the juvenile, and does not become secretive in habit. *G. maculatus,* which breeds in river estuaries on grass-covered, upper-tidal flats, differs from the other four diadromous species in its spawning habits. Although little is known about the spawning habits of these four species, they seem likely to breed in or near the adult habitats.

In some populations of *G. fasciatus,* and many of *G. brevipinnis,* the life cycle is restricted to fresh water. What changes have occurred in the life history of *G. fasciatus* subsequent to becoming landlocked in the Kaihoka lakes is presently unknown, but the population in Lake Okataina, and the many populations of *G.*

brevipinnis in upland lakes, have a life history pattern in the lakes similar to the diadromous populations in the sea, although the juvenile life is of course lacustrine instead of marine.

Two small lacustrine species, *G. usitatus* and *G. gracilis,* are landlocked derivatives of *G. maculatus.* What is known of the life histories of these species suggests that they continue to spawn in the autumn, but that the diadromous habits have been eliminated. An Australian landlocked derivative of *G. maculatus* shows peculiar modification of the life history of the parental species, but this is not known to have occurred in these New Zealand species (see Pollard, 1966: 14).

The remaining seven New Zealand galaxiids have fewer, larger eggs, they spawn mostly in the winter and spring, complete their entire life histories in flowing, fresh water and do not appear to migrate. There is no whitebait stage in any of them, nor do they seem to exhibit any metamorphosis. How these species have been derived from the diadromous species is not obvious, but it seems likely that the easily dispersed diadromous species are ancestral to at least some of the entirely freshwater species.

New Zealand was heavily glaciated during the Pleistocene (See Fleming, 1962: 89), and the rivers must have been much colder than now. Species which were probably lowland or coastal during the glaciations must have become adapted to cold water and are now probably those found in upland-alpine areas, where temperatures are about as cold as they were coastally during the glaciations. By spawning in the spring, the young of these species develop and undergo early growth in somewhat less severe conditions than would be the case if they spawned in the autumn, as the diadromous species do. The possession of a marine migratory phase by the diadromous species may be an alternative strategy for surviving through the cold winter. Development in the sea gives them access to the prolific marine plankton, and in the

winter, the oceanic water temperatures during the glaciations would have been less extreme than river temperatures, making it worthwhile for the young fishes to spend the winter in the sea. The occurrence of five diadromous species in New Zealand and only three in warmer Australia perhaps supports this argument, and analysis of the life history patterns of South American Galaxiidae will be interesting, since *Galaxias* species occur in the far southern regions of Chile and Argentina.

The migratory stages of the Northern Hemisphere salmonoids appear to behave in a similar fashion. Kendall (1935: 11) noted that *Salvelinus* species in the far north are essentially marine species, entering fresh water occasionally for food and reproduction. Further south, "the marine forms gradually disappear, becoming almost or quite exclusively freshwater inhabitants at the southern end of each range." The presence of a marine migratory stage in both the salmonids and galaxiids may be connected with attempts to avoid the rigors of the extremely low temperatures and icing of freshwater habitats.

Egg number and egg size show good correlation with the alternative life history patterns. The species with marine life history stages have more numerous eggs, usually several thousand. High fecundity is perhaps related to high mortalities of larvae in the marine plankton and further mortality due to loss by dispersal in the sea and the hazards of making a migration from the sea into fresh water. Also related to increase in egg number, and the fact that the larvae enter the highly productive marine plankton, are the comparatively small eggs, with little yolk. The non-lacustrine species which are restricted to fresh water, in which mortality during the juvenile stages may be lower, and which don't suffer from dispersal by ocean currents (although they are carried downstream by river currents), have much fewer eggs, usually numbering only a few hundred

red. Increased survival of the fewer eggs is favored by larger size; this may be advantageous in rapidly flowing water in giving the freshly-hatched larvae a better chance of resisting downstream dispersal and also to compensate for any paucity of food available to very tiny fishes in rapidly flowing water. Greater yolk volume is advantageous because the larvae can depend on this for food for a longer period, and also because the larvae, hatching into swiftly flowing water, are larger and thus better fitted to maintain their position in the stream and find shelter from the currents.

Subjective observations indicate that the same relationship between egg size and egg number exists in the New Zealand Eleotridae. The species with fluviatile adults but marine or lacustrine juveniles—*Gobiomorphus huttoni* (Ogilby), *G. basalis* (Gray), *G. gobioides* (Valenciennes), and *Philypnodon hubbsi* (Stokell)—have much smaller and more numerous eggs than the single species which lives and breeds entirely in flowing, fresh water—*P. breviceps* Stokell.

This suggests that for diadromous species, high larval mortality due to predation and dispersal plus high food availability in a productive marine plankton have favored selection for numerous, small eggs. In contrast, in the non-migratory fluviatile species, somewhat lower larval losses due to less predation and dispersal, and greater ability to resist dispersal as a result of increased larval size at hatching, have favored selection for fewer, larger eggs, which carry more nutritive yolk.

There is a very clear relationship between life history patterns and range in the New Zealand Galaxiidae. It was previously pointed out (McDowall, 1966a: 16) that the fact that "certain species of *Galaxias* have marine whitebait is reflected in their New Zealand distribution." The present study, in altering the taxonomy of some problematical species, has further strengthened this observation. Reference to the

Table 7. Distribution of New Zealand Galaxiidae.

	Whitebait Juvenile	North of North Island	South of North Island	West Coast South Island	East Coast South Island	Offshore Islands	Localized
G. argenteus	X	X	X	X	x	X	–
G. fasciatus	X	X	X	X	x	X	–
G. postvectis	X	X	X	X	x	–	–
G. brevipinnis	X	X	X	X	X	X	–
G. maculatus	X	X	X	X	X	X	–
N. diversus	–	X	–	–	–	–	–
G. divergens	–	x	X	X	–	–	–
N. apoda	–	–	X	X	–	–	–
G. vulgaris	–	–	–	x	X	–	–
G. prognathus	–	–	–	x	x	–	–
G. paucispondylus	–	–	–	–	X	–	–
N. burrowsius	–	–	–	–	X	–	–
G. gracilis	–	–	–	–	–	–	X
G. usitatus	–	–	–	–	–	–	X

X = Present, widespread.
x = Present, restricted.
– = Not present.

species distribution maps (Figs. 7, 10, 20, 22, 25, 33) shows that the widespread species, and those which are found on the offshore islands, are the species which also have marine whitebait stages. *G. maculatus*, *G. brevipinnis*, *G. fasciatus*, *G. argenteus*, and *G. postvectis* have all been found over large areas, where suitable habitats have been searched, and various of these species have been recorded from the Cavalli, Chicken, Little Barrier, Mercury, Kapiti, Arapawa, D'Urville, Stewart, Chatham, Auckland, and Campbell Islands. *G. maculatus* is present in Australia, Tasmania, Lord Howe Island, New Zealand, and the Chatham Islands, Chile, Patagonia, and the Falkland Islands. There can be no question that the wide range of this species is entirely a result of the existence of the marine whitebait stage.

In marked contrast, the non-migratory species have a much more restricted range. The two main islands of New Zealand are divisible into four somewhat dubious, but presently useful, faunal regions. The North

Island is divided centrally by the volcanic plateau, with large areas north and south of it. The areas east and west of the Southern Alps-Kaikoura Mountains mountain chain are separated by these high mountains. In Table 7, the New Zealand Galaxiidae are listed and their presence or absence in each of the four areas noted. This table illustrates dramatically the difference between the diadromous and non-migratory species in breadth of range. It also shows that the species in the latter group are restricted to one or two, occasionally three, of the so-called faunal regions. Two species have very localized distributions, occurring in only one water body. Five species occur solely in one area or extend marginally into a second; e.g., *G. prognathus* and *G. vulgaris* are found primarily to the east of the Southern Alps, but both species appear to have crossed the divide once, in the vicinity of the Lewis Pass, and have entered the upper reaches of the Buller River System, flowing to the west (see p. 424).

Two species occur widely in two faunal regions and one of these, *G. divergens*, is marginally present in a third. It should be noted that both these species are present primarily in the south of the North Island and the west of the South Island. Consideration of the range of some other animals, e.g., *Paranephrops planifrons*, the fresh water crayfish, suggests that the Buller-Nelson-West Coast area of the South Island has close biogeographic affinities with the south of the North Island. Fleming (1962) showed that for most of the Tertiary the two islands of New Zealand were connected across Cook Strait, and his map for the Pleistocene shows that the river systems from the Wellington area in the North Island and the northwest of the South Island were confluent in the now submerged area. The distribution patterns of *G. divergens* and *N. apoda* are thus easily explained in terms of land bridging of Cook Strait and indicate that these two areas have close faunal affinities.

Data on species range make it quite clear that the presence of a marine stage has resulted in a broad geographical range. This same factor, the presence of a marine stage in the life history, has also imposed some restriction on inland penetration and altitudinal range. Species that migrate up rivers from the sea are excluded from areas that the migratory juveniles are unable to reach in their migration. The extent of restriction in altitudinal range varies from species to species and is, in part, related to the climbing ability of each species. Climbing ability is, in turn, related to certain morphological adaptations (see "Adaptive radiation," p. 414). *G. maculatus* appears to be completely confined to lowland and coastal streams and rivers, and has been found to be virtually incapable of climbing a low artificial weir about six feet high across the Waikanae River (McDowall, 1964b: 145). Other diadromous species present in the river (*G. fasciatus, G. postvectis,* and *G. brevipinnis*) were found above the weir and were thus obviously climbing it. *G. brevipinnis* whitebait have also been observed climbing up the vertical concrete face at one end of an aqueduct beneath a road (K. F. Maynard, pers. comm.). *G. brevipinnis, G. argenteus, G. fasciatus,* and *G. postvectis* juveniles have been found to be extremely troublesome to keep in captivity because of their propensity for climbing out of aquaria. This ability is important to species migrating upstream from the sea, especially in a mountainous country like New Zealand; amongst the diadromous species, those which penetrate far inland, especially *G. brevipinnis,* are also good climbers.

The origin and age of the New Zealand galaxiid fauna

It is now fairly generally believed that the Galaxiidae, together with the Retropinnidae and Aplochitonidae, are derivatives of the primarily northern salmonoid fishes. The osteology of these three southern families suggests that they are probably derived from some very early osmeroid stock.[1]

The three families are restricted to the Southern Temperate Zone, except for a single, more tropical species in New Caledonia (this species is found only in cooler, mountain lakes). The northern salmonoid families which seem to have given rise to the southern families are found only in the Northern Temperate and sub-Arctic. Thus, this quite large and diverse group of fish families is confined to the temperate zones, exhibiting bipolarity at the subordinal level. They are cold water fishes and seem to be excluded from more tropical areas by temperature. If this is so, it is difficult to imagine how the southern families could have been derived from the northern families unless either there was a period in the early Tertiary when tempratures were considerably cooler than now, or southward dispersal took place by tropical submergence. Until the Pliocene cooling which led to the glacial periods, temperatures in the Tertiary are thought to have been warmer than now. Fleming (1962: 66) suggested that New Zealand was warmer than now during the late Mesozoic and remained warm well into the Tertiary. If, as suggested, the salmonoid fishes are limited in range by temperature, tropical submergence seems to be the most likely means of traversing the tropics. Hubbs (1953: 325) conjectured that the three southern families are "pre-Tertiary relicts of groups that failed to persist in the tropics." The basis for Hubbs's conclusion is not clear. Certainly none of the living generalized salmonoids are tropical, or even subtropical. Existing temperature limitations and inferred temperatures since the end of the Mesozoic suggest that occurrence of salmonoids in the tropics is unlikely at any time since the radiation that produced the southern salmonoid families occurred.

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[1] The evidence on which this supposition is based is discussed elsewhere (McDowall, 1969; see also Weitzman, 1967).

Where the southern families entered the Southern Hemisphere is also not very clear. The existing predominance of the Galaxiidae, as well as the Retropinnidae, in the Australasian region suggests that dispersal occurred across the tropics in southeastern Asia. More than 20 galaxiids are recorded from Australia, 14 from New Zealand, 4–5 from South America, but only one from South Africa. These details suggest that South Africa is a most unlikely source of origin and dispersal, and that it is, rather, the end of a chain of dispersal areas, under the influence of the west wind drift. If South America were taken as the center of dispersal, and if we use existing currents (see Fell, 1967), then the Australasian fauna must then have been derived by dispersal eastwards via South Africa, and again, the presence of only one species there suggests the improbability of this having taken place. *G. maculatus* is present in Australia, New Zealand and South America, but not South Africa, and this suggests that it originated in Australia and spread eastwards. For such reasons, I think that Australia is the most likely area for the origin and dispersal of the family Galaxiidae, and that the New Zealand fauna was derived from the Australian one.

How the galaxiid fishes have dispersed is fairly clear, although the wide geographical range of the Galaxiidae has puzzled many ichthyologists and zoogeographers. As recently as 1950, Stokell discussed means by which the family could have dispersed by land routes. Long ago, however, Boulenger (1902: 84), noting that "most text books and papers discussing geographical distribution have made much of the range of a genus of small fishes, somewhat resembling trout, the *Galaxias*," pointed out that some species are not restricted to fresh water. I have earlier (McDowall, 1964a) analyzed the derivation of the New Zealand freshwater fish fauna, and at that time I concluded that since all the families in the fauna (including the Galaxiidae) contain species that have

marine stages, their presence in New Zealand is simply and clearly explained by trans-oceanic dispersal. The existence of at least seven diadromous species of *Galaxias* (two in Australia, four in New Zealand, and one further species in both) strongly supports the hypothesis of oceanic dispersal, and the range of one of these species—*G. maculatus*—suggests that this dispersal continues (McDowall, 1966a). It appears that the East Australian current, which travels down the east coast of Australia and which may impinge on much of the west coast of New Zealand, supplies a suitable mechanism for dispersal from Australia to New Zealand (see Fell, 1962, 1967). However, it is uncertain how much this current affects the New Zealand region. Burling (1961: 51) suggested that the Tasman current, which flows on to the west coast of New Zealand, is derived from the East Australian current as it turns eastward towards the central Tasman Sea. The similarities between the marine faunas of southeast Australia and New Zealand (see Moreland, 1958, for fishes, and Fell, 1967, for evidence of recent dispersals) support the probability of water transport in this manner. However, Dr. B. V. Hamon (pers. comm.) suggested that eddies that break off from the East Australian current may be a mechanism by which water is carried across the southern Tasman Sea, but that at present there is no evidence to suggest that these eddies persist over such distances, and it is not known how long it would take such eddies to travel across.

Fleming (1962: 105) concluded that "during the early Cretaceous, the geanticline west of the New Zealand geosyncline could have extended north to New Caledonia," but "at no time is there any evidence for direct trans-Tasman connection with Australia." There seems little likelihood of a suitable land bridge between New Zealand and Australia. In 1963 (p. 382) Fleming pointed out that if "the podocarps, *Sphenodon*, the frog *Leiopelma*,

many invertebrates, *Nothofagus,* and perhaps the ratite birds walked into New Zealand . . . . across an Antarctic land bridge from South America lasting at least into the middle Cretaceous, we are left with problems almost as great as those solved. What kept the land dinosaurs, the early mammals and snakes from New Zealand?" On this basis, he gave "wavering support to the view that the dispersal of the Paleoaustral organisms, like that of the Neoaustral element, was across the sea." The whole idea of land-bridge dispersal of the Galaxiidae to New Zealand must be discarded; or looking at the problem from a different perspective, the present range of galaxiid fish gives absolutely no support for any land connection between New Zealand and any other land area at any time.

The age of the New Zealand galaxiid fauna is uncertain. The comparative sizes of the families of freshwater fishes in the New Zealand fauna (and none of them looks like a relict)—Geotridae, one species; Galaxiidae, 14 species; Retropinnidae, six species; Aplochitonidae, one species; Anguillidae, two species; Eleotridae, six species; Cheimarrichthyidae, one species —suggest that the Galaxiidae may form the oldest existing element in the freshwater fish fauna. The fossil record is of little help in dating the fauna, since the only galaxiid fossils are from the Upper Pliocene of Fraser's Gully, Kaikorai near Dunedin. No other fossils of any freshwater fishes are described from New Zealand, and no galaxiids are recorded from other regions. Romer (1966: 356) listed a *Galaxias* from the Oligocene of New Zealand, but the original record of this fossil is unknown to me in any galaxiid literature. The Oligocene of New Zealand was a period of extreme marine transgression, and there was very little emergent land (see Fleming, 1962: 74); freshwater deposits would be very limited in extent, if present.

The fossil record thus provides little information on the age of the family, or on how long it has existed in New Zealand. The number of species in New Zealand, and their distribution pattern, suggests initial arrival in the early or mid-Tertiary, certainly considerably before the period of the Fraser's Gully deposit. Romer (1966: 355) recorded salmonoid fishes back to the Upper Cretaceous, and one existing genus—*Thymallus*—in the Eocene. Osmeroid fishes from which the southern families seem to be derived are dated back to the Miocene. The prospect that the salmonoid fishes were present in the Australasian region as long ago as the beginning of the Tertiary must be recognized.

Adaptive radiation

Since the family Galaxiidae is by far the largest family of freshwater fishes in New Zealand, it probably represents an old element in the fauna. However, to what extent the present fauna represents the fauna of the Tertiary is not clear, and it may be that as a result of changes in land form, marine transgressions, and glaciations during and after the Tertiary, the present fauna is only a surviving remnant of a more extensive fauna. But there are no apparent relicts in the fauna. If the neochannoid species represent a distinct radiation, independent of the Tasmanian mudfishes, they would seem to constitute an old element in the fauna, but the distribution of the three New Zealand neochannoid species seems to be a result of obvious geological events, like the rise of the South Island mountain chains and the central North Island volcanic plateau, or the marine transgressions of the earlier Tertiary. If these are old species, they give no indication of significant extinction.

All the New Zealand freshwater fishes fall into species groups (or are the sole representatives of their family in New Zealand). And those species that have no close relatives in the New Zealand fauna have such relatives in Australia. The relationships and distribution patterns of the New Zealand freshwater fishes give no

evidence for the occurrence of much extinction, and most appear to be rather recent in origin. Apart from man-caused extinction, I see no reason to suspect that the New Zealand freshwater fish fauna, including the Galaxiidae, has ever been any more diverse or speciose than it is at present.

The galaxiid fauna has been built up in two ways—by invasion from Australia and by speciation in New Zealand. As I discuss in the section "Species groups and phylogeny" (p. 418), I think that invasion has played an extremely important role in the development of the fauna, and I think that evolution of the fauna in the New Zealand region has been slow and rather ineffective in populating New Zealand's fresh waters.

There is little question that the fauna is depauperate. Comparison of New Zealand's freshwater fish fauna, comprising about 31 species, with that of Japan, 127 species (Okada, 1960), or the British Isles, 72 species (Regan, 1911), suggests that the freshwater habitats of New Zealand are far from saturated and that there is considerable scope for invasion. (This is not meant to imply that potentiality exists for the introduction of game fishes, since the past results of such introductions to New Zealand indicate that they may have serious effects on the existing fauna (McDowall, 1968a).) It is not surprising that the fauna is depauperate. New Zealand has been geographically isolated from other land since at least the end of the Mesozoic (Fleming, 1962: 105), and this has completely prevented the invasion of New Zealand by primary or secondary freshwater fishes. What is interesting is the failure of the species arriving to radiate in the semi-vacant and highly productive freshwater habitats of New Zealand. I find it surprising that so much of the fauna is adventive and not a result of diversification of stocks in the New Zealand region.

There are no herbivores in the New Zealand freshwater fish fauna. This is almost certainly a result of the scarcity of aquatic vegetation, which is itself at least partly related to the mountainous character of many New Zealand rivers. Furthermore, none of the species can be classed as piscivorous, data showing that some species may occasionally take fish, but that it is not customary (McDowall, 1965b, 1968b, Hopkins, 1965). Stream invertebrates make up the bulk of the food of all species, except for very large examples of the long finned eel, *Anguilla dieffenbachii* (Cairns, 1942: 139).

Galaxiids have invaded a wide variety of habitat types. Rapid-water species tend to be more slender in form, but are, in their general characters, similar to slack-water species. A few, e.g., *G. brevipinnis*, *G. postvectis*, have a receding lower jaw, which suggests adaptation to feeding off the stream bottom. Conversely, *G. prognathus* has a conspicuously protruding lower jaw, and this is a very obvious adaptation for picking invertebrates off the under sides of rocks. There is some variation in dentition, but only in the degree of development of lateral canine teeth in the jaws and of mesopterygoidal teeth in the roof of the mouth.

Most species are solitary and secretive. They are usually found in heavy cover and have great thickening of the fins, which provides resistance to fin damage when the fish swim amongst rocks and logs; these species also almost invariably have emarginate to truncated caudal fins. The pectoral fins are usually placed low lateroventrally on the trunk, a modification probably related to bottom resting and feeding habits. *G. brevipinnis*, in which this is most pronounced, also has deep corrugations on the lower surfaces of the pectoral fins, which may help the fish to grip the stream bottom and maintain its position in the very rapid flow of its habitat. In contrast, the few species that shoal and live openly in pools have more membranous fins, the pectorals are positioned much higher laterally on the trunk, and the caudal has a definite fork. It seems justi-

fiable to interpret these characters as being related to the shoaling or midwater habits. The functional nature of the differences is perhaps least obvious in the caudal fin, although in shoaling groups, e.g., clupeids, the caudal fin is invariably forked, whilst in secretive, cover-dwelling groups, e.g., umbrids, the caudal fin tends to be truncated or rounded. Furthermore, the juveniles of the diadromous species are shoaling in habit and have forked caudal fins, the fins only becoming emarginate as the fishes mature and become solitary and seek cover. A further character related to shoaling habits, and also characteristic of shoaling fishes in general, is silvery coloration on the abdomen, present in the New Zealand Galaxiidae only in *G. maculatus* and its shoaling derivatives.

The low position of the thick, fleshy pectoral fins has served as a preadaptation for climbing. The diadromous species, which have the pectoral fins inserted low on the lateroventral trunk are much better climbers than *G. maculatus*, in which the fins are higher. The fact that the pectoral and pelvic fins are about flush with the ventral trunk and have the lamina facing downwards seems very important in the great climbing ability of species like *G. brevipinnis*, *G. fasciatus*, and *G. postvectis*.

The differences between the diadromous and freshwater species in egg size and number is discussed in the section on life history patterns (p. 409). A further difference between these groups of species is the length of the gill rakers. The five diadromous species and two lacustrine species (*G. usitatus* and *G. gracilis*) have long, well-developed gill rakers, whereas most other species have much shorter, sometimes irregularly-spaced rakers. The tendency towards gill raker reduction is especially evident in the slender alpine species, *G. divergens* and *G. prognathus*. These differences correlate with the existence of a shoaling, plankton-feeding phase in those species with long rakers and the lack of such a phase in the fluviatile species.

One of the most distinctive character divergences in the New Zealand Galaxiidae is the probably neotenic retention of shoaling habits and the associated morphological peculiarities seen in *G. maculatus*. It is notable, though, that this apparently did not originate in the New Zealand region, but its presence in New Zealand represents an independent invasion from Australia.

The three neochannoid species have not hitherto been discussed in relationship to the radiation of the family. This is largely because their adaptations represent a radiation into the most peculiar niche occupied by members of the family in New Zealand, though this group, too, might have originated in Australia and dispersed to New Zealand. If not, these species represent the most striking example of inventiveness in the New Zealand galaxiid fauna. There are three species that occur in swamps, swampy creeks, and sometimes springs, and that have an ability to aestivate during droughts. Common morphological characters, like loss or reduction of the pelvic fins, reduced eyes, long nostrils, low median fins that are more or less confluent with the caudal fin, rounded caudal fin, are interpreted as modifications for a semi-burrowing existence.

The limited extent of the radiation of the New Zealand Galaxiidae suggests that they are a conservative group. In this they are similar to their Northern Hemisphere relatives—the Salmonidae and Osmeridae—which are principally cold water predators of rather uniform morphology, although their habits may vary. The differences that have developed in the Galaxiidae are usually variations on the theme of solitary, secretive invertebrate predators. The most persistent variation involves adaptations to different water types—placid pools in stable bush streams to rushing torrents in open, unstable shingle rivers—and the persistence or loss of the marine whitebait juvenile stage. In the case of habitat differences, morphology shows little variation

—usually some elongation and depression in rapid-water species. The only obvious differences associated with the presence or absence of a whitebait stage are those related to survival of the progeny (egg size and number) and feeding (length of gill rakers). These characters are those likely to be most affected by selection, since the low saturation of the New Zealand freshwater habitat leads to little interspecific competition—selection is mostly intraspecific and related to feeding and reproductive efficiency.

The conservativeness of the group is seen in its failure to become open living and benthic, like the eleotrids, which are almost certainly more recent invaders. They have not become mid-water pool-living species like the species of *Retropinna*, but instead, when found in pools, generally skulk in marginal cover. They have mostly been unable to remain in streams that have lost their forest cover, and except in localities that may have been naturally alpine grassland in Central Otago and alpine Canterbury, streams without cover are mostly populated by eleotrids, eels, and sometimes *Retropinna*. Nor have they been particularly successful as lacustrine species. *G. argenteus* and *G. fasciatus* are known as adults from very few lakes; *G. brevipinnis*, although commonly found in lakes in the juvenile stages, is rarely lacustrine as an adult.

The exception to all these is *G. maculatus* and its derivatives. They are shoaling, open-living, pool-dwelling species, which have persisted in streams without cover and have become partly lacustrine. But apart from the landlocking in *G. usitatus* and *G. gracilis*, these characteristics do not represent evolution in the New Zealand region but are a product of dispersal of *G. maculatus* from Australia. The dominating impression acquired from studying the New Zealand Galaxiidae is that they have adapted their basic structure and way of life to a variety of water conditions, and have pursued their invertebrate-feeding habits in these.

Analysis of sympatry in the family in New Zealand shows that there is likely to be little interspecific competition. *G. usitatus*, *G. gracilis*, *Neochanna diversus*, and *N. apoda* have never been collected from the same water bodies as other galaxiids. This is also true for most of the range of *G. divergens*, but this species is known to be sympatric with *G. prognathus*, *G. vulgaris*, and *G. brevipinnis* in two localities. *G. vulgaris* is found in some waters with *G. brevipinnis* below some of the South Island alpine lakes and with *G. paucispondylus*, *G. prognathus*, and *N. burrowsius* in a few Canterbury rivers.

The species that exhibit broad sympatry are the diadromous species—*G. maculatus*, *G. brevipinnis*, *G. argenteus*, *G. fasciatus*, and *G. postvectis*—plus *G. prognathus* and *G. paucispondylus*, both of which are known from very few rivers, and occur together and with *G. vulgaris*, *G. brevipinnis*, or *G. divergens*. There is a likelihood here of competitive species interactions, and in these species there are some signs of significant niche differences; this is a profitable area for further study.

The sympatry of the diadromous species is interesting in that these species appear to be a product of successive invasions of the New Zealand region. All five species probably occur together in mixed associations as juveniles in the sea, and they migrate upstream from the sea together (McDowall, 1966a). It is unusual, however, for the adults to be taken from precisely the same habitat type, even though several species may be present in the same pool-rapid series in just a few yards of stream. The habitats of *G. fasciatus* and *G. argenteus* are especially similar, but the common association of these species in nature suggests that some habitat divergence is likely. A detailed study of microdistribution in river systems where various of the species are sympatric may provide interesting data

on niche and the effects of sympatry on niche breadth.

Species groups and phylogeny

The New Zealand Galaxiidae are easily divided into a series of small, distinct, species groups. These vary in their compactness, but they combine species that appear phylogenetically more closely related to each other than any species in one group is related to those in other groups. Although it is possible to list characters that unify the species groups, many of these are adaptive. However, the general form and habits of the species in these groups show such similarities that they seem to be valid. The species groups are as well defined by the gaps between species groups as by the similarities between the contained species.

There is a group of small, slender species that are somewhat compressed in form and have membranous fins, a long-based anal (Fig. 45, B, f, g, h), a forked caudal, and shoaling habits. They vary somewhat in their reproductive cycle, but otherwise form a compact group. *G. maculatus* (Fig. 21) is one of the more distinctive New Zealand *Galaxias* species, and probably stands far apart from other New Zealand species, except its immediate derivatives. The fact that *G. maculatus* is present in Australia, Tasmania, New Zealand, the Chatham Islands, South America, and the Falkland Islands has important implications in an analysis of the phylogeny of the family in New Zealand. The only way this species could have attained its present distribution is by trans-oceanic dispersal. Existing ocean currents indicate that *G. maculatus* probably originated in Australia and dispersed eastwards, in the west wind drift. If this is so, then *G. maculatus* has no direct affinities with other New Zealand species groups. Since populations from these widely separated land areas are conspecific (Stokell, 1966: 76, McDowall, 1967b) it seems that the original dispersal occurred quite recently.

Comparison of *G. maculatus* with *G. usitatus* and *G. gracilis* (see McDowall, 1967a: 3) shows that the latter two species, each of which is confined to one small lake, are landlocked derivatives of *G. maculatus*.

Although the three species look very similar, there are marked differences in body proportions and meristic characters. The divergence which has taken place since *G. usitatus* and *G. gracilis* became landlocked indicates that the species are plastic in their general morphology. *G. gracilis*, for instance, appears to have traversed the full range of vertebral number seen in the New Zealand Galaxiidae. *G. maculatus* represents a maximum, with 59–64, and *G. gracilis* a minimum for the family in New Zealand, with only 47–50. The argument that this is evidence that *G. gracilis* is not closely related to *G. maculatus* conflicts with the evidence of their obvious similarity; and in view of the known relationship between vertebral number and developmental temperatures, basing affinities on vertebral number must be regarded as suspect. *G. gracilis* has diverged further from *G. maculatus* than has *G. usitatus*. This is in accord with the apparent ages of the small lakes in which these species are found. Lake Rototuna (*G. gracilis*) occurs in well-stabilized, rolling sand dunes, once covered with bush, and at an altitude of about 90 m. It is probably older than Lake Waiparera (*G. usitatus*), which occurs in still shifting sand dunes, no more than 36 m above sea level.

Some workers, e.g., Whitley and Phillipps (1940: 229) and Phillipps (1940: 39), have suggested that *G. castlae* Whitley and Phillipps (=*G. brevipinnis* Günther) and *G. paucispondylus* are also landlocked derivatives of *G. maculatus*. Present understanding of the nature of the fauna suggests that this is most unlikely, and I think that *G. maculatus* and its two derivatives belong in a quite distinct species group.

A second species group includes three very similar large, stout-bodied species,
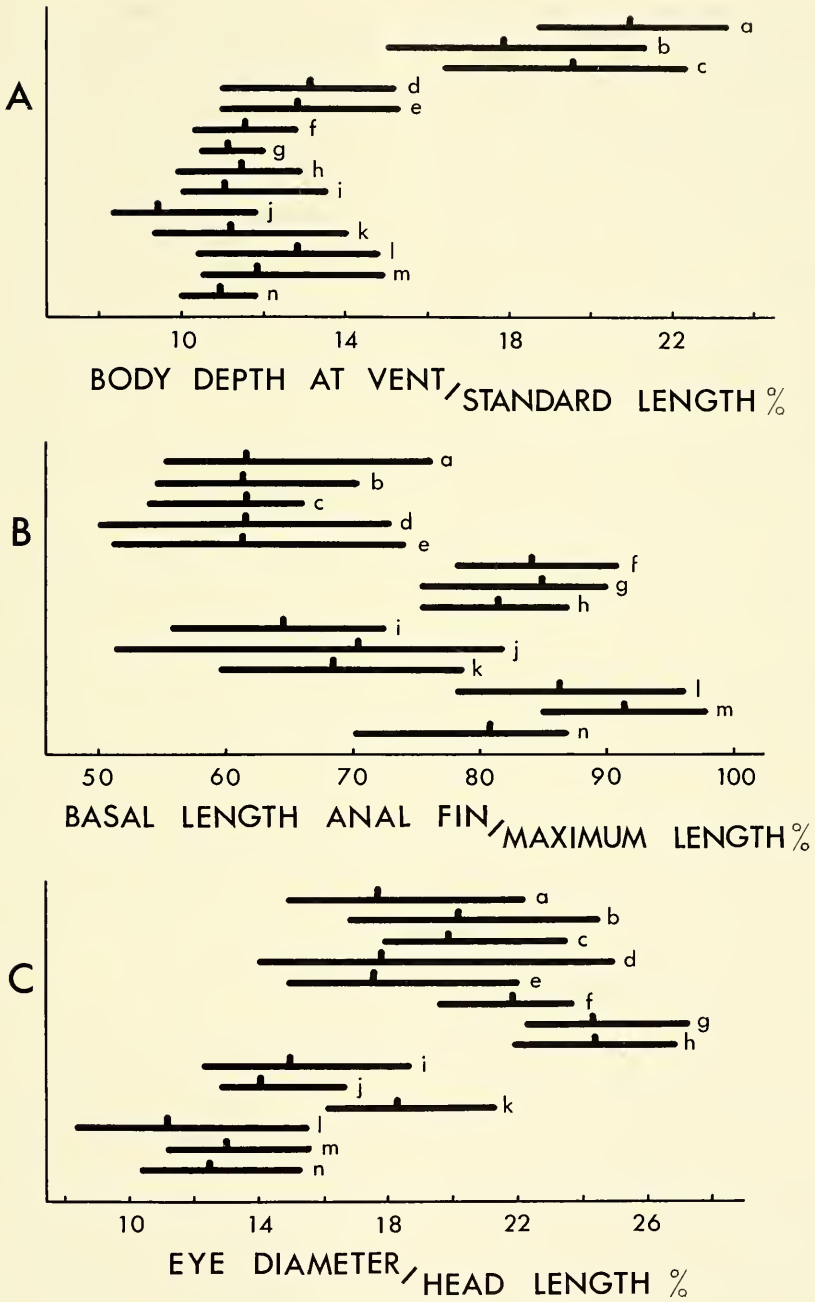
Figure 45. Species groups in the New Zealand Galaxiidae, as indicated by body proportions. a, *Galaxias argenteus*; b, *G. fasciatus*; c, *G. postvectis*; d, *G. brevipinnis*; e, *G. vulgaris*; f, *G. maculatus*; g, *G. gracilis*; h, *G. usitatus*; i, *G. paucispondylus*; j, *G. prognathus*; k, *G. divergens*; l, *Neochanna apoda*; m, *N. diversus*; n, *N. burrowsius*.

which are mostly lowland dwelling. These species, *G. argenteus*, (Fig. 4), *G. fasciatus* (Fig. 6), and *G. postvectis* (Fig. 9), form a compact group with their long, truncated to emarginate caudal fins, expansive dorsal and anal fins, and very long pectoral and pelvic fins, deep bodies (Fig. 45A, a, b, c), short and very deep caudal peduncles, and rather long, broad heads. The accessory lateral line is developed, and in all three, a large, dark, blue-black blotch above and behind the pectoral fin base is present. They all spawn in the autumn, are diadromous, and are found in rather similar habitats. The three species have almost identical ranges, and their characters strongly suggest common ancestry. But explaining their divergence within the New Zealand region is a problem for which I see no solution. It is difficult to imagine how allopatry could have developed, since all three species occur together in a common marine pool, migrate into fresh water in mixed species shoals, and are found together in the adult habitats. It is no simpler to see how speciation could have occurred had all three species remained sympatric. Even if a satisfactory model for sympatric speciation were to be constructed, this would necessarily involve habitat, reproductive, or behavioral differences of a nature and degree that seem to be lacking in these species. The only alternative is that these fishes invaded New Zealand from Australia several times, giving rise to the three stout-bodied species. Their great predominance on the west coast of New Zealand (see Fig. 7) suggests that they have evolved in the swift, rocky bush streams there, rather than in the very different plains streams of the southeast, where they are largely absent.

In the Australian galaxiid fauna, *G. truttaceus* Valenciennes shares many of the morphological characteristics of the stout species and is a suitable ancestral type; as it has a marine whitebait juvenile (Lynch, 1965), it also has the necessary dispersal ability. Since the larval stages of the three

New Zealand stout-bodied species are believed to spend many months in the sea, giving them plenty of time to disperse from Australia, and since the East Australian-Tasman currents may be favorable for such dispersal, multiple dispersal of fishes ancestral to the stout species is quite comprehensible. Castle (1963: 13) suggested that the New Zealand freshwater eels (*Anguilla* spp.) probably spawn somewhere in the tropical Pacific, northeast of the New Hebrides; it would thus be the action of these currents which bring the leptocephali to New Zealand coasts—and they come in colossal numbers. The efficacy of these currents in dispersing fishes to New Zealand from the northeast seems demonstrated.

Skrzynski (1967) and others have reported the following New Zealand species from the Chatham Islands, 420 miles east of New Zealand: *G. fasciatus*, *G. argenteus*, *G. brevipinnis*, and *G. maculatus*, as well as *Gobiomorphus huttoni* (Ogilby), *Retropinna retropinna* (Richardson), *Anguilla australis schmidtii* Phillipps, *A. dieffenbachii* Gray, and *Geotria australis* Gray. Thus, unless these fishes have been on the islands since they were connected to mainland New Zealand, there must have been a great deal of dispersal to the islands from New Zealand, demonstrating considerable dispersal powers.

If *Galaxias argenteus*, *G. fasciatus*, and *G. postvectis* have each reached New Zealand from Australia, with a common ancestry there, these dispersals must have been at sufficiently separated intervals to permit reproductive isolation to develop between successive invasions. In comparison with the ideas of earlier workers on galaxiid fishes, that they must have reached New Zealand by means of land bridges, Gondwanaland, continental drift, etc., the idea of dispersal on several occasions is radical. But it is clear that there was a separate dispersal to bring *G. maculatus*; perhaps it is necessary to envisage independent dispersals for each of the three

stout-bodied species. If so, then the minor habitat and morphological differences between the three species are likely to be a product of interspecific competition forcing the three rather similar, sympatric species to specialize in some way. There is something inherently dissatisfying about the hypothesis of multiple invasions without any radiation of the group in New Zealand, but the formulation of a model allowing their speciation in New Zealand, either sympatrically or involving the development of geographic or other barriers to gene flow, eludes me.

Looking at the entire New Zealand fish fauna, it appears that it is almost entirely an invasion of fauna, with little speciation in the New Zealand region. Moreland (1958) has shown that only 30 per cent of the fauna is endemic. Since 7 per cent of the fauna is freshwater, and about 94 per cent of the freshwater fishes are endemic, it follows that only about 24 per cent of the marine fauna is endemic. Analysis of the fauna from Phillipps (1927a) shows that about 100 families, 200 genera, and 318 species occur in the fauna; thus there are two genera per family, and one and one half species per genus. Nearly one half of the genera have only one New Zealand species. Both the low endemism and the structure of the fauna suggest that the fauna is derived more by invasion from outside than from evolution within the New Zealand region (there is only one doubtful endemic marine fish family), and it is necessary to postulate fishes crossing the Tasman Sea a great number of times. Since, according to Moreland (1958: 28) 31 per cent of the species are presently shared with southeast Australia, recent trans-Tasman crossings must number in the vicinity of 100. The Galaxiidae, with their long-lasting oceanic, pelagic stages are admirably fitted for this dispersal, which may have occurred several times.

G. brevipinnis has many characteristics also found in the stout-bodied species, but it is much more slender (Fig. 45A, d). In addition to being widespread in New Zealand, it is present on the Chatham Islands, 420 miles east of New Zealand, the Auckland Islands, 290 miles south of New Zealand, and Campbell Island, 150 miles southeast of the Auckland Islands. It has a marine whitebait and thus has potentiality for transoceanic dispersal, and its range in the New Zealand region shows that it is probably a more effective disperser than any other species of *Galaxias*, except *G. maculatus*. As indicated in discussing the taxonomy of *G. brevipinnis*, I think that *G. weedoni* should become a synonym; if these two species are not conspecific, they are certainly very closely related, and *G. brevipinnis* is derived from *G. weedoni*.

Assuming that *G. brevipinnis* originated in the Australian region, it is necessary to explain its present distribution. As with the other species, it must have arrived in the New Zealand region in the East Australian and Tasman currents. Dispersal of fishes from New Zealand to the Chatham Islands does not appear too difficult, judging from the number of fishes that have succeeded in doing so. The difficult dispersal seems to be that to the sub-Antarctic islands—Campbell Island and the Auckland Islands. Dispersal from New Zealand is opposed by the west wind drift, which flows from west to east, south of New Zealand, with a substantial northern displacement, i.e., the Ekman drift (Burling, 1961, see his chart 1), which flows northeast from the sub-Antarctic islands, towards the south and east of New Zealand. It is possible that *G. brevipinnis* represents a direct dispersal from Australia to the islands; such a dispersal could have occurred if fishes in the East Australian current were picked up by the deeper west-east flowing west wind drift. The existence of a somewhat more extensive land area to the south of New Zealand, perhaps until late in the Tertiary, makes dispersal directly to the southern islands more plausible.

If *G. brevipinnis* was present in the sub-Antarctic islands prior to the Pleistocene

glaciations, its survival there during the glaciations becomes a critical question. If it became exterminated by the glacial ice cap, judging by existing current patterns, re-invasion of the islands from New Zealand would have been difficult, if possible. Gressitt (1964b: 11) reported that Campbell Island (the more southern of the two island groups) was "mildly glaciated during the Pleistocene . . . . there are cirques as well as glacial valleys but no proof of a continuous ice sheet." Gressitt (1964a: 548) thought that the fauna represented a depauperated fragment of an ancient subcontinental fauna, with over-sea colonization. Illies (1964: 215) examined the Plecoptera of Campbell Island, finding that "the existence of running freshwater environments on the island must have lasted at least since the break-down of land connections," i.e., for the present discussion, through the glaciations. This being the case, *G. brevipinnis* could probably have survived there too.

G. vulgaris is very similar in general form and appearance to *G. brevipinnis.* None of its body proportions are greatly different, although it is a little less depressed in the head region and the jaws are nearer equal in length. In the area where the two species are sympatric, it has fewer vertebrae, fewer rays in some fins, and shorter gill rakers, but these are all minor differences. The most significant difference is in the life history: *G. vulgaris* spawns in the spring and has no marine whitebait stage. This might seem a major difference, which precludes relationship between *G. vulgaris* and *G. brevipinnis;* yet Pollard (1966: 14) found that an apparently recent, landlocked derivative of *G. maculatus* in Victoria, Australia, has changed from autumn to spring spawning and from downstream to upstream migration prior to spawning. And this life history modification has been accompanied by very little morphological differentiation.

G. vulgaris is virtually restricted to the eastern side of the Southern Alps in the South Island, but it is very widespread in this area. This suggests that it must have evolved since the rise of the Southern Alps in the late Miocene and Pliocene. Its similarity to *G. brevipinnis* suggests that it is a derivative of this species, but how it diverged is unclear. *G. brevipinnis* and *G. vulgaris* are presently widely sympatric, since the former occurs in many lakes above the rivers in which the latter is found. The lacustrine populations of *G. brevipinnis* almost certainly post-date the Pleistocene glaciation. Apart from these lake populations, *G. brevipinnis* is very rare in the east of the South Island, and is probably sufficiently rare for isolation of some population(s) in one or several of the river basins which lack lacustrine populations of *G. brevipinnis* in the upper reaches. Such a happening may have allowed divergence of populations leading to *G. vulgaris.* Isolation may have been possible in some Canterbury rivers that do not flow directly into the sea, but disappear into coastal gravel, but this seems unlikely to have been a long-term condition in any particular river, such as would allow speciation.

There is a compact group of three small, slender, alpine species. They are confined to fresh, flowing water and do not have an obvious juvenile-adult metamorphosis. They are widespread in the southern half of the North Island and the northwest of the South Island, and extend over the Southern Alps into alpine Canterbury. This group comprises *G. divergens, G. paucispondylus,* and *G. prognathus.* Body proportions like slender trunk, very long and slender caudal peduncle, anterior dorsal fin insertion, short head with broad, shallow gape, short anal fin, bring these species together. Meristics are generally low. Of particular interest is the number of pelvic rays. *G. divergens* consistently has six rays, and although the two other species usually have seven, a high proportion of *G. paucispondylus* examined had six rays. In both *G. prognathus* and *G. paucispondylus* it was found that when there were seven

rays present, the ray in each fin closest to the ventral midline was commonly much reduced and often unbranched. This is interpreted as illustrating the trend towards reduction in the number of pelvic fin rays, a process that has become absolute at six rays in *G. divergens*. In these species, the anteriormost of the interorbital pores on the head has migrated to a position very close to the posterior nostril. In *G. divergens*, and sometimes in the other two species, the opening of this pore has become confluent with that of the nostril. This is a trend not seen in any other New Zealand species; the pore and nostril are always well separated. A further significant character that unites these species is the loss of the postcleithrum in the pectoral girdle. Occasionally there is a barely staining splint, but usually the postcleithrum does not appear in alizarin-stained adult specimens. It is present, though, in all other New Zealand galaxiids. In addition, the supraethmoid has a characteristic irregular shape, the palatine lacks the process that in other galaxiids runs along the side of the face lateral to the mesopteryoid, the mesopterygoid and metapterygoid do not meet in the posterior corner of the orbit but are separated by a band of cartilage, and there are no processes on the basioccipital. The species in this group exhibit some sympatry, *G. divergens* and *G. paucispondylus* being completely allopatric, but *G. prognathus* more or less bridging the geographic break between the other two.

There is little question that these species have a common ancestry, probably in a species similar to *G. paucispondylus* or *G. divergens*, which are more generalized than *G. prognathus*. Our present knowledge of their ranges may not be sufficiently complete to allow valid conclusions about their evolution. In particular, the two disjunct localities known for *G. prognathus* strongly suggest that further localities remain to be discovered in the intervening area, especially since the rivers there are superficially similar to those in which *G. prognathus* has already been found.

The present range of this species group suggests that the ancestral form had spread over the Wellington-Nelson-Buller region during or since the uplift of the Southern Alps. Their preference for cold alpine streams indicates that they may have evolved during the cold Pliocene-Pleistocene periods, and Fleming (1962: 81) considered that the "climax of the Kaikoura orogeny" occurred during the Pliocene. The existence of a single population (of *G. divergens*) in the east of the Volcanic Plateau far north of other known populations is a problem. Fleming showed that the marine transgression of the Miocene persisted into the Pliocene, covering the southern half of the North Island, from Taranaki to northern Hawke's Bay, except for the Wellington area, which was emergent and connected with the Nelson-Buller district. The northern population is conspecific with *G. divergens*, in which the pelvic fin ray number is only six, suggesting that this species must have spread north as the southern half of the North Island emerged towards and during the Pleistocene. It seems unlikely that this disjunction is a result of any earlier geological event, like the Miocene transgression; it is probably due either to destruction of the populations in the intermediate area—inland Hawke's Bay and northern Wairarapa—by the known, recent volcanic activity, or to incomplete knowledge of the range of the species.

G. divergens occurs in the south of the Bay of Plenty, the Wellington Province on both sides of the mountain ranges, and the northwest of the South Island as far south as the Buller River System at Maruia. *G. prognathus* is presently known only from the Buller River System at Maruia and the Rakaia System over on the eastern side of the Southern Alps. *G. paucispondylus* occurs in several river systems along the eastern side of the Alps.

This distribution pattern gives the im-

pression of a single, widespread species whose range became fragmented by the development of geographical barriers. If the ancestor of these species was widespread in the Nelson-Buller-northeast Canterbury regions during the rise of the Southern Alps, it would have been divided into two isolated series of populations by the mountains. Such a division would have sufficed to allow the divergence that has taken place between *G. paucispondylus* and *G. divergens.*

G. *prognathus*, in its remarkably elongated lower jaw, is, in some ways, the most specialized species of *Galaxias* in the New Zealand fauna. Its specialization suggests that it may have been in competition with another, similar species, like *G. paucispondylus* or *G. divergens.* It is almost certainly derived from one of them and the most recent species of the three.

G. *vulgaris* is distributed east of the ranges in the South Island, but it has invaded the west, in the upper Buller River System, in the Maruia River. This seems likely to have occurred since the rise of the Alps, for two reasons. First, the Maruia population shows very little divergence from those on the east, certainly less than that seen between various populations in the east; in other words, its derivation from the east seems to be very recent. In addition, the fact that *G. vulgaris* is present only in one western river system, and the fact that this river drains the lowest existing pass in the northern alps, suggests that *G. vulgaris* has crossed the alps from east to west, and recently.

The derivation of *G. prognathus* from either *G. divergens* or *G. paucispondylus* seems most simply accounted for if we presume that the parental species of *G. prognathus* was able to cross the alps. This would have brought *G. divergens* and *G. paucispondylus* into sympatry. If they had only recently become reproductively isolated, competition is likely to have been intense, forcing one of the species, probably the invader, to specialize, leading to

G. *prognathus.* Since *G. prognathus* is now recorded from both sides of the Alps, it must also have recrossed the divide, and if it did evolve in competition with either *G. paucispondylus* or *G. divergens,* it is not very obvious on which side it is likely to have evolved. If it evolved on the east and has reinvaded the west, there is nice agreement with the distribution pattern of *G. vulgaris,* since both species are known in the west only from the Maruia River, in the upper reaches of the Buller River System, near the Lewis Pass. It appears too much of a coincidence that both these species are known in the west only from this one river, and that the river's headwaters drain the most easily crossed pass in the Alps. Stream capture seems quite feasible in the Lewis Pass area, and I am advised (P. M. Johns, pers. comm.) that there is a swampy area in the pass between the headwaters of the rivers on each side. I think that both *G. vulgaris* and *G. prognathus* have quite recently crossed from east to west and that *G. prognathus* probably evolved in the east. If so, I suspect that *G. prognathus* will be found in further alpine Canterbury rivers, particularly the upper tributaries of the Waiau, Hurunui, and Waimakariri Rivers.

An alternative hypothesis, which is feasible but without obvious support from physiographic changes, is that the two species in the east evolved in separate river basins and have subsequently become sympatric, as the rivers wandered back and forth across the Canterbury Plains and various pairs of rivers became confluent for a time. These river changes must be the mechanism behind the present broad range of *G. vulgaris,* but, inasmuch as they have not sufficed to produce speciation in *G. vulgaris,* it seems unlikely that isolation of any basin has been of sufficient duration to allow the contained populations to evolve reproductive isolation.

The final species group comprises the three species of *Neochanna*—*N. burrow-*

sius, N. apoda and *N. diversus*—which present a distinctive facies. They have an elongate and rounded trunk, somewhat blunt and little depressed head, small eye (Fig. 45C, 1, m, n), and a prominent development of the tubular anterior nostril, which may extend forwards beyond the upper lip. The dorsal and anal fins (Fig. 45B, 1, m, n) are rather long and low, with extremely thick, fleshy bases, the caudal fin is much rounded, and the peduncle flanges are very strongly developed, more or less confluent with the dorsal and anal fins. In *N. apoda* and *N. diversus* the pelvic fins and girdle have disappeared, and there are usually no mesopterygoidal teeth. The process of reduction is less complete in *N. burrowsius*, which has very small pelvic fins with only four or five rays, and only a few, small mesopterygoidal teeth, or none at all. Stokell (1945: 132) discussed the question of whether these three species form a natural phylogenetic unit, or whether their similarities are a case of convergence. He concluded that "if *burrowsius* is to be regarded as indicating the line of descent of *Neochanna* from *Galaxias,* it might be expected that a dominantly four rayed form, or a form lacking ventral fins but retaining vestiges of the pelvic bones would exist to indicate a further stage in the process of degeneration." As Stokell found, there is no such intermediate stage, and this is what students of evolution have commonly, if not normally, found. In this instance, it seems to indicate that a widespread species, ancestral to all three, had reached a stage of modification about equivalent to that exhibited by *N. burrowsius.* After the populations making up *N. burrowsius* were isolated, the modification continued, producing the other species of *Neochanna,* again probably from a common stock. A cursory examination of the three species shows that they are very similar to each other, certainly far more similar to each other than any one is to any New Zealand species of *Galaxias.*

It seems likely that the common ances-tor of the neochannoid species was widespread in New Zealand in the Miocene as the marine transgression began. From this time onwards, the transgressions and great orogenies that followed would have fragmented its range. The populations now known as *N. burrowsius* would have been isolated from populations in the north and west by the rise of the main South Island mountain ranges in the late Miocene and Pliocene, and were perhaps restricted to the present small pocket in the Canterbury Province by the cold of the glaciations. Following this, the populations in the north and west lost the already reduced mesopterygoidal teeth and pelvic fins. During the Pliocene, the marine transgression covered most of the southern half of the North Island, and the transgression would have isolated populations—in the north of the North Island, leading to *N. diversus,* and in the Nelson-Buller-West Coast area, leading to *N. apoda.* Land connections between the North and South Islands lasting into the Pleistocene would have allowed *N. apoda* to reach the southern North Island, if it was not already present.

The preceding discussion suggests some probable species groups and their phylogenetic relationships, and thereby establishes possible terminal branching points in the phylogeny of the species (Fig. 46). It seems almost certain that three of these branching systems, those containing (1) *G. maculatus* and its derivatives, (2) the stout-bodied species, and (3) *G. brevipinnis* and *G. vulgaris,* originated independently in Australia; *G. maculatus* occurs in Australia, the stout-bodied species seem to be derived from *G. truttaceus,* and *G. brevipinnis* is derived from *G. weedoni* or is conspecific with it.

There are two other very closely knit and distinctive species groups in the New Zealand fauna. There is no evidence to suggest where the slender, alpine species originated. The neochannoid species have counterparts in the Tasmanian fauna, presently treated by Scott (1936: 160) as two

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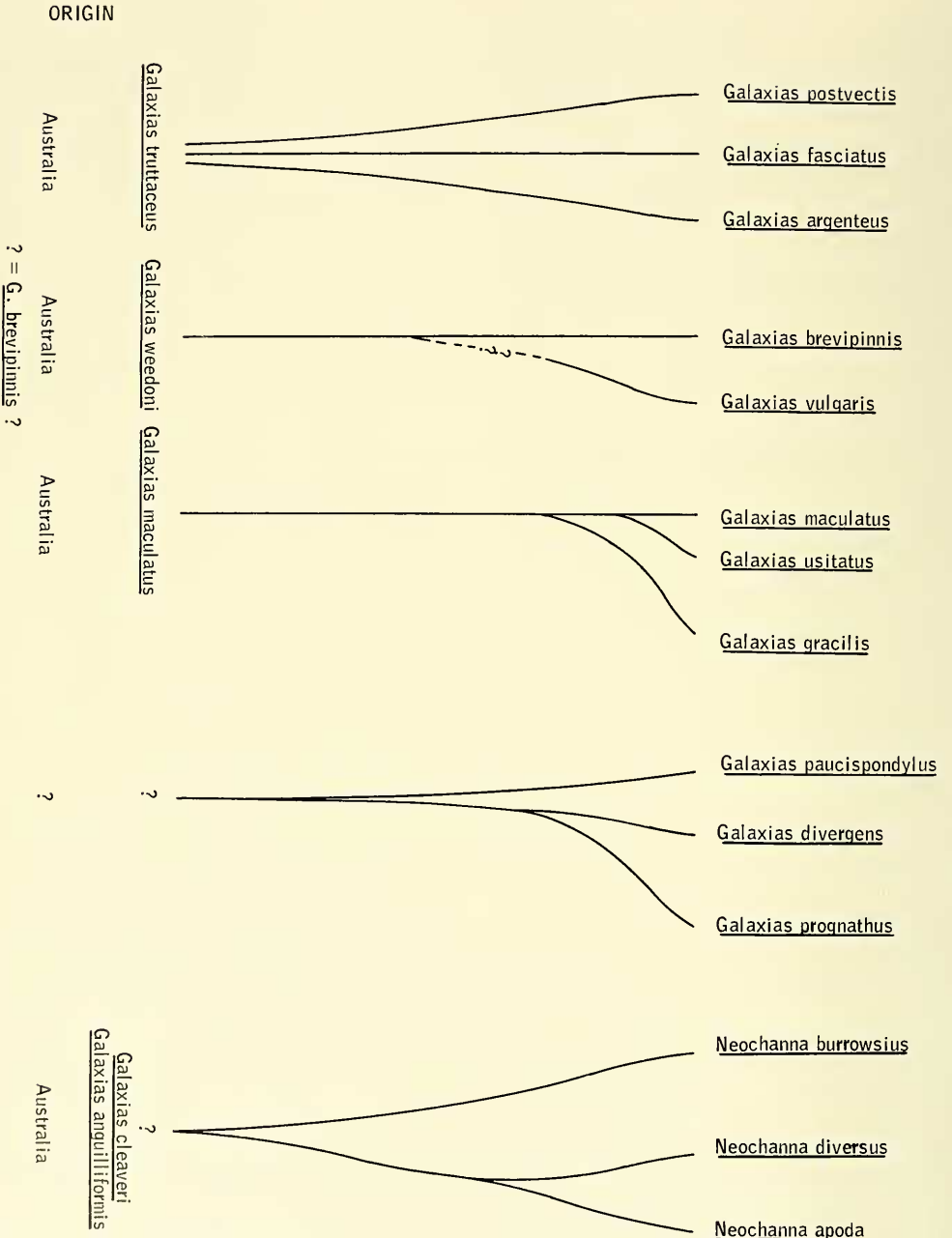
Figure 46.   Suggested phylogenetic relationships of the New Zealand species of *Galaxias* and *Neochanna*.

species of *Saxilaga.* If, as workers like Fleming (1963: 382) claim, the ratite birds, *Sphenodon, Leiopelma,* and other animals dispersed to New Zealand across the sea, then it is possible that a neochannoid species, even though it does not possess a definite sea-going stage, could have rafted or otherwise dispersed to New Zealand.

Presently, nothing is known about the euryhalinity of either New Zealand or Tasmanian species of this group, but it is certain to be much greater than that of *Leiopelma*, a small frog. If the Australian species, treated by Scott (1936) as the distinct genus *Saxilaga* (also said to include *N. burrowsius* from New Zealand and *G. globiceps* Eigenmann from Chile), have a common origin with *Neochanna* in New Zealand, it may be necessary to alter the generic arrangement of these species. The answer does not, however, seem to lie in whether *G. cleaveri* Scott and *G. anguilliformis* Scott belong in the genus *Saxilaga*, but in whether or not it is preferable to regard them as species of *Galaxias*, showing evolutionary trends towards *Neochanna*, or to include them in *Neochanna*, as a distinct radiation of "mudfishes." If these species do form a natural grouping, it seems natural to include them all in *Neochanna*. The inclusion of *G. globiceps* in this assemblage is supported neither by Eigenmann's description nor by his figure of the species. Before these problems can be clarified, the osteology of these species needs study.

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ADDENDA

1). Since this work was completed, an extensive re-analysis of the taxonomy of *G. maculatus* and its lake derivatives in 16 lakes in Australia, New Zealand, and South America, has been made. This analysis suggested that *G. usitatus* McDowall (p. 382) is best regarded as a local race of *G. maculatus*, although the validity of *G. gracilis* McDowall (p. 384) is confirmed (McDowall, In Prep.).

2). Study of adult specimens of *G. weedoni* Johnston supported tentative suggestions (p. 364) that this species is a junior synonym of *G. brevipinnis* Günther, which is thus shown to have trans-Tasman range (McDowall, In Press, Records of the Dominion Museum, New Zealand, vol. 7).

3). A recent checklist of the fishes of New Zealand by G. P. Whitley (Australian Zoologist, vol. 15, 1968, pp. 1–102) listed as valid several *Galaxias* species synonymized by myself and earlier authors, and is inaccurate and misleading.